THE

AMERICAN NATURALIST

VOL. XXXV. *December, 1901.* NO. 420.

REGENERATION IN THE EGG, EMBRYO, AND ADULT.

T. H. MORGAN.

THE term "regeneration" has come to mean not only the replacement of a lost part, but also the production of a whole organism from a piece of an animal or of a plant. There are even other phenomena that must be included under the same term, such as, the production of a part different in kind from the one lost, and also, as I shall try to show, those cases in which a part of an egg or of an embryo produces a whole or a part of an organism. It appears that there are two principal modes by which regeneration takes place. The first and more familiar process is by means of the formation of new tissue at the exposed region, followed by the development of new organs out of this new tissue. In order to distinguish this mode from the other, we may call it "epimorphosis." The second mode of regeneration is brought about by the transformation of the entire piece into a new form. For this process I have proposed the term "morphallaxis." These two modes of regeneration are not sharply separated, for we find in some forms — noticeably in the planarians — both processes combining to produce a new organism.

It has been only within the last few years that zoölogists have discovered that parts of the embryo, or even of the unsegmented egg, have also the power of producing new, whole organisms, and while this process has been here and there brought into relation with the process of regeneration, — especially by Roux and by Barfurth, — yet up to the present time no systematic analysis has been carried out in order to see how far the regeneration of pieces of an adult organism and of pieces of the egg are similar or identical processes. It is the special object of this paper to examine further into this question.

I.

In order to make clear our subsequent comparison between the development of pieces of the adult and of the egg and embryo it will be necessary in the first place to review briefly a few well-known facts. It has been stated that there are, in general, two modes by which a piece of an adult may regenerate: (*A*) either by the development of new tissue at the exposed regions, — epimorphosis; or (*B*) by transformation of the old part into a new form, — morphallaxis.

(*A*) *a*. Furthermore, we find under the first category that when a small piece of the organism is removed (1) the organism regenerates as much as is lost; but (2), on the other hand, the small piece does not generally make the whole organism, if in fact it regenerates at all. As examples of these different processes I may cite the following cases. If the leg is cut from a newt, the larger piece — the newt — makes a new leg, but the leg does not make a new newt. If the head is cut from a snail, the snail makes a new head, — if the cut has not been made too far back, — but the head does not make a new snail. If it be objected that in both cases the smaller piece dies before regeneration can begin, I may cite another experiment made on the earthworm. If a few anterior segments are cut off, they do not make a new worm, although the piece may remain alive for a long time without showing any signs of regeneration, and during this time the larger piece, from which the anterior end had been cut off, may have

completely replaced the lost smaller part. It may also be stated that the result is not dependent upon a lack of material in the small piece, for the process of regeneration does not even begin, and, as other experiments have shown, there is certainly enough material in the small piece for regeneration to have been carried out to some considerable extent.

b. The other case in this category is that in which the large piece produces only the distal end of the part removed and, therefore, less than the part cut off. For instance, if more than five segments are taken from the anterior end of the earthworm, still only five are regenerated, and the intermediate region is never regained. In the planarian, if more than the head is cut off, only the head is *at first* regenerated, but in this case the intermediate, or missing region, is made good by subsequent changes that take place in the region behind the new head and in front of the old part. A similar thing happens when the posterior end is cut from an earthworm. At first only a small part comes back, consisting of the end-piece — the telson — and a few segments, but by subsequent growth new segments are intercalated near the posterior end just in front of the telson. Again, if the tail of a fish is cut off near its base, there appears at first only *a small new part that assumes the characteristic form of the tail, even before the new part has grown out to the level at which the tail was cut off.* Subsequently, by a process of continuous growth, the entire tail is replaced.

(*B*) *a.* The second mode in which the process of regeneration takes place is, as I have said, by the transformation of the entire piece into a new organism. This is known to occur only in those forms that we speak of as the lower animals, but in which, nevertheless, a high degree of specialization may exist. The most familiar case, and the one longest known, is that of hydra. Trembley saw that small pieces may change into new, whole animals, and subsequent investigators have observed the same thing. They have not, however, pointed out specifically that new tissue is not added at the cut-ends, but from personal observation I can state that there is no special development of new tissue in these regions. The entire piece changes over

into the new form. Another example of the same process, first made known by Bickford, is that of Tubularia. In this form it is even more evident that a piece of the stem may be transformed into a new hydranth without new tissue forming beyond the level of the cut-end.

In planarians we find not only new tissue developing at the cut-end, but also a transformation taking place in the old parts. The Protozoa also regenerate by changing over the old part into a new form. From the figures given by Gruber and others there can be little question that the piece is transformed directly into a new whole, although this important fact has not been emphasized by those who have written on the subject. A piece of Stentor, for example, if it contains one or more nodes of the macronucleus, produces a new Stentor having the characteristic form, but on a smaller scale. I have repeated this experiment on Stentor, and have found that small pieces produce new organs that are of proportionate size.

In these cases of morphallaxis, just described, the small pieces change over into the characteristic form of the species, *i.e.*, they are new wholes of smaller size. They may subsequently grow to the full normal size, and even produce sexual organs. On the other hand, there is known at least one case in which very small pieces produce not a whole form, but only a part of a whole. It has been shown that very short pieces of the stem of Tubularia may produce only the distal end of the hydranth, *viz.*, a proboscis. Other experiments show that, nevertheless, the material out of which the proboscis develops is totipotent. This problem will be more fully discussed later in another connection. The result also suggests direct comparison with those cases in which only a part of what has been removed is regenerated out of the new tissue that appears at the cut-end, as when only a few anterior segments regenerate in the earthworm after the removal of a much greater number. In fact, I think it may be shown that there is something more than a mere similarity between the two cases, and that they both result from the action of the same factors.

We may next examine some of the cases in which a part of the egg, or of the embryo, produces an entire organism. The

earliest observation of this sort was made by Haeckel in 1870. Pieces of the embryo of a jellyfish were found to produce each a new smaller embryo which gave rise to an entire organism. This discovery attracted little or no attention at the time, because the important theoretical questions that are involved were not appreciated. Without treating the facts in the order of their historical sequence I shall describe a few other results that have a direct bearing on the questions before us.

The development of isolated blastomeres is one of the simplest cases of the kind. If the first two blastomeres or cells of the egg of the sea-urchin be separated from each other, each continues to segment, in most cases as though it were still a part of a whole. There is produced a half blastula open at the side that corresponds to the region at which the other blastomere lay at the two-cell stage. The half sphere next closes in to become a whole sphere of half size, and from this time onwards the embryo continues to develop as a symmetrical whole, passing through the later stages as does the normal, whole embryo.

These results show that after separation of the blastomeres each continues to develop for a time in the same way that it would have done had it remained in contact with its fellow; but the process of half development is only carried through the cleavage stages, and then a new change takes place, initiated by the closing of the open side, and a new whole of half size is established. It is this process of closing of the opening and the subsequent whole development of the half piece that resemble the changes that take place in the regeneration of pieces of adult animals.

In other species of sea-urchins the isolated blastomeres behave in a somewhat different way. In Sphærechinus the cleavage is not so obviously a half cleavage, or at least while the first divisions may be more or less like those of a blastomere that remains in contact with its fellow, yet there is not formed an open half sphere, but the blastomeres close in as they are formed. A whole embryo of half size is also produced in this case.

In another sea-urchin, Toxopneustes, it has been found that after separation of the blastomeres the cleavage may proceed

at once as a whole, *i.e.*, the isolated blastomere divides in the same way that the whole egg divides, and not as it would have divided had it remained in contact with its fellow. The blastula is closed from the beginning. Later, as in the other cases, a whole embryo develops.

These and other experiments seem to show that the form of cleavage of the egg is the result of an arrangement or structure of the protoplasm, and that in some cases this same arrangement is retained after the separation of the blastomeres; while in other cases the protoplasm may rearrange itself at once into a new whole, in which the arrangement of the parts is symmetrical and like that of the whole egg. The blastomere divides in consequence in the same way as does the egg.

The closing in of the half blastula of Echinus presents certain obvious resemblances to the closing in of pieces of adult animals. Several writers have supposed that in both cases this change is due to a simple physical rearrangement of the material, but it is, I think, not altogether improbable that at least one other factor is also present. I base my opinion on the study that I have made of the closing in of pieces of Tubularia, of hydra, and of the closing of large wounds made in the side of very young tadpoles. While the closing in seems to be the result, in part, of the physical property of the semifluid substance to become round, or more symmetrical, it seems also to involve certain contractile phenomena of a different sort. The cells that are in contact draw towards each other as a result of their own movement or contractility. There may be also certain tactic phenomena present. At least, if we cannot show positively that some such factors may be at work we have at least no right to exclude them in the present state of our knowledge as possible factors in the result.

After the closing of the half blastula has taken place we find that the piece no longer behaves as a part, but as a new whole. We must assume that it has become a symmetrical or whole structure. Let us look somewhat further into this question.

We have seen that in the case of the egg the change that takes place in a piece, making the piece symmetrical, may be brought about by a simple physical rearrangement of the

substances of the protoplasm; but after the piece has been divided into parts or cells the contents of each cell is separated from that of its neighbor by the cell-walls which we have come to look upon as barriers preventing free interchange between the cells. In many cases, however, an actual continuity of the protoplasm from cell to cell has been demonstrated, and it has been recently shown that connections may be established during the cleavage period between neighboring cells. We shall not go far wrong, I think, if we assume that the protoplasm throughout the embryo is a continuous structure, and that it is not shut up in protoplasmic-tight compartments. How, then, from this point of view can we look upon the changes that take place in an unsymmetrical piece so that it becomes symmetrical? Can we regard the first step to be the same as in the piece of an egg, *i.e.*, to be the outcome of a symmetrical rearrangement of the material or substances contained in the egg? We may think of this as possible, but the change in itself would not be sufficient to account for the subsequent events, unless we assume that it leads to the symmetrical organization of the living substance itself, for on this rather than on the gross contents of the protoplasm the subsequent changes seem to depend. That this must be so is shown, I think, by the following considerations.

Numerous experiments have demonstrated that any part of the egg may produce a whole embryo — provided, of course, that it contains the nucleus and is large enough. The substances contained in the different parts of the protoplasm are very similar throughout the egg, although there may be more or less of one or of another sort in each region. Since any part of the egg can produce an embryo we cannot regard the presence or absence of any of these substances as of fundamental importance; hence it is probable, I think, that the result depends on the protoplasm rather than on the substances it contains.

The structure of the egg is a symmetrical one, as its development shows; a piece of the egg retains at first its old structure in most cases as its cleavage demonstrates, but it may later become also symmetrical, as the later changes

prove, and we are led to ask, What is the nature of this symmetry[1] or organization that exists in the protoplasm of the egg, and which may appear in the protoplasm of a part of the egg? The problem is all the more difficult to understand when we find that an egg that has divided on a radially symmetrical plan may produce a bilateral embryo. It is probable, however, in such cases that a bilateral structure is really present from the beginning of the cleavage, but that the factors that are at work during the cleavage are not necessarily those that determine the bilateral organization of the embryo. In some cases, as in the frog's egg, a careful examination even of the early cleavage stages shows that a bilateral organization is present in the protoplasm, although the form of the cleavage may appear in many cases to be radially symmetrical.

In order to answer our question in regard to the nature of the organization we should have to know more of the nature of development itself. All we can do at present is to examine some of the implications that are involved in the assumption, and at least attempt to make clear our position. The new axial relations that are established in the piece present certain interesting relations. If the original organization was a bilateral one that corresponded, let us assume, more or less with the plane of the first division, then an isolated blastomere has at first only the organization of a half, or rather contains the factors that lead to a half development. In other words, it has no median plane of symmetry, yet later such a median plane is established. It is this change, taking place in the isolated part, that we are forced to assume, that gives us one of the most interesting and also important problems with which the student of experimental embryology has to deal. We know of nothing similar taking place in inorganic nature. The most obvious change that may seem to approach this is in the formation of an entire crystal from a piece, but in this case there is never any change in the position of the original axes that the piece has inherited from the old crystal; there is no rearrangement

[1] The term "symmetry" does not, perhaps, express the idea entirely, since an egg with an asymmetrical cleavage must be regarded as having also a definite organization.

and, hence, the essential condition is absent. Our conception of the structure of a magnet must be also fundamentally different from the ideas involved in the organization of the egg. It is true that any piece of a magnet at once becomes a whole magnet of smaller size, and this occurs in the smallest pieces that it is possible to obtain. On the other hand, the change in the organization of a piece of the egg is a relatively slow one, and it can take place only in a relatively large piece of the substance. If it be objected that these differences are only trivial ones, and not essential, still it can be shown, I think, that we must hold entirely different views of the nature of the polarity of a magnet and the organization of the egg. Our conception of the polarity of the magnet rests on the idea that it is the sum total of the polarities, or, perhaps, of the orientation of the minutest elements, the molecules, of which the magnet is made up, while our conception of the organization of the egg is exactly the reverse (or at least I shall try to show that we must really believe this to be the case), and we must think of the entire egg as a whole and not the sum total of an infinite number of smaller wholes. We may claim, I think, that this property of the egg substance of forming itself into a new whole is peculiar to the living protoplasm and is a property that we do not find, or have not found as yet, in inorganic, or perhaps we may go further and say in dead, matter. If we choose to call this property of living matter a vital factor in the sense that it is not found in matter that is dead there can be, I think, little objection to so doing. If the statement seems to be arguing in a circle, we may state more simply that those properties of living things that are not shown by non-living things we shall call vital properties. We may add that we cannot be sure, at present, whether these vital factors will conflict with our present ideas of causality or not; they seem rather to be, however, new causal phenomena peculiar to certain organic substances or compounds, but it would be out of place here to examine further into these difficult questions.

I have dwelt somewhat at length on this topic because, as I shall try to show, an analysis of the phenomenon that takes place when a piece of an adult animal (hydra, for

example) changes over into a new, whole organism, leads us directly to the same conclusion.

A ring cut at any level from the body of hydra closes its open ends quickly, and in the course of a few days it elongates and assumes the typical proportions of this form. At the time of the operation the piece was a part of a definite organization, yet it afterwards becomes itself a whole structure. The material of which the piece is composed must be totipotent, since any piece may make a whole structure. The results demonstrate that although the piece must be regarded as a part of a whole organization before it was removed, yet after its removal it becomes itself a whole organism. This fact shows that there is no contradiction in our regarding the entire egg as also having a definite structure, or as being an organized whole, and yet any piece of it may become a new whole. This conclusion is of some importance because, at first, students of experimental embryology were inclined to go too far and assume that, since any piece of the egg could become a new whole, therefore, the egg itself must be regarded as a very simple structure. The experiments with hydra show that the egg *may be* as highly organized as is an adult animal, and yet a piece produce a new whole. It is scarcely necessary to add that the results do not show that the egg *is* so highly organized but only that it may be thought to be so without contradicting the results of the experiments.

I pointed out in my Woods Hole lecture of last year (1899) that from whatever part of the body a piece may be cut it will still be different in its different parts, in so far as one part was nearer the anterior end and another nearer the posterior end of the animal. And similarly for the sides of pieces of a bilateral animal, one part will always have been nearer than another to the median plane, etc. These differences suffice, I think, for us still to form a *causal* conception of how the new axial relations are attained, since the differences always present will be the basis on which the subsequent rearrangements take place, and the results of observations show, in fact, that the anterior end of the new organism comes from the anterior end of the pieces, etc. We may infer that a similar change takes place

in the reorganization of the egg; and we can form here also a causal conception of the change, although we may admit that it is a change different from anything that we know of in inorganic matter.

We may next examine some other results connected with the development of pieces of the adult and of the egg. It has been stated that a small piece of the stem of Tubularia sometimes produces only a partial form, — a proboscis, or a proboscis with reproductive organs, or a hydranth without a stem. The development of these partial structures occurs only in small pieces. The production of a proboscis, for instance, takes place only in pieces that are much smaller than the average size of the hydranth-forming region of a long piece of the stem. An entire hydranth without a stem may, however, develop from pieces that are much longer than the minimal size of the hydranth-forming region of short pieces. The point of special interest is that the development of the proboscis takes place in pieces whose material is totipotent, *i.e.*, the material can produce any part of a hydranth or of a stem. We may restate the result by saying that there is a stronger tendency, especially in the more distal parts of the stem, to form the full-sized organs than to form the whole structure in a reduced form.

These results with small pieces of Tubularia suggest at once a comparison with those cases in which a part of an egg develops into a part of an embryo, and not into a whole one of smaller size. This is most strikingly shown in the ctenophore egg and also in the egg of a snail, Ilyanassa. It has been found that, if the first two or first four blastomeres of the ctenophore egg are isolated, each not only divides as a part, but each develops into an incomplete embryo that lacks, in the case of the one-half blastomere, a half or nearly half of the entire structure, and in the isolated one-quarter blastomere lacks about three-fourths of the entire structure, etc. If pieces are cut from the fertilized but unsegmented egg of the same animal the embryos that develop from the nucleated pieces are also often incomplete. The results indicate that the phenomena are due to a lack of regulative power, or power of rearrangement

in the egg; perhaps to a lack of lability in the protoplasm, so that it fails to reorganize itself into a new whole. The result is not due to the smallness of the piece, for under certain conditions, not yet understood, a smaller piece than a half or a fourth of the egg may make a whole structure. We must, therefore, look upon the egg of the ctenophore as totipotent in all its parts, in the same way that the sea-urchin's egg is totipotent, but an incomplete embryo develops from a piece, since the egg *after* fertilization has not the power, under ordinary circumstances, of rearrangement or regulation. It is conceivable that at a different temperature or in a slightly different medium the protoplasm of the piece might rearrange itself so that an entire embryo would develop.

If we think of the embryo as organized in the protoplasm of the egg in the sense of there being present a definite structural arrangement of the protoplasm, then when the blastomere of the ctenophore egg is isolated there is simply a lack of change. If, on the other hand, we think of the egg at the beginning of cleavage as being organized only in so far as the cleavage is concerned, the later organizations appearing afterwards, then we must think of the half organization of the embryo as being induced by the half form of the cleavage, or the half form of the isolated part. The half development would, in this case, not be due to a lack of change, but to the appearance after cleavage of a half organization. If we adopt the latter alternative we can compare the development of the one-half ctenophore embryo with the production of a part of a hydranth in a small piece of Tubularia. In both cases a part of a structure is formed on account of the form or size of the piece in material that is totipotent. If, on the other hand, we adopt the first alternative we find the two processes different, unless it could be shown that towards the distal end of the piece of Tubularia a new hydranth may be organizing before the old hydranth is thrown off. The removal of a piece taking place at this time, each piece continues to develop in the determined direction. Since, however, only distal organs develop from such pieces at several levels we see that this view is insufficient by itself to give a satisfactory solution.

In regard to this latter point it seems that the development of an incomplete structure in Tubularia is not such an isolated phenomenon as it appears to be at first sight, but can be brought into harmony with certain other known results. For instance, when more than five segments are cut from the anterior end of the earthworm only five, as a rule, come back at whatever level of the anterior end the cut may be made. The amount of material that is formed at the cut-end, before differentiation begins, is about the same at all levels, and this gives, I believe, an insight into the phenomenon. There is for the earthworm, also, a lower limit of organization for the formation of the head, or of a ring of the body, and the same new part is formed at each level, because the amount of material that is at first formed over the exposed end is the same. We must look upon this material as totipotent, but the number of rings that it produces is limited, on account of the amount of material present and of the necessary connection that exists between the lower limit of organization and the volume of matter.[1] The analysis leads us in both cases to the supposition that the results are somehow dependent on the ultimate structure of the protoplasm from which arises the structure that we can see. The development of a proboscis from a small piece of the stem of Tubularia indicates that there is a quantitative element that comes into the problem, and this conclusion is directly in line with the conclusion that we reach from a study of pieces of minimal size of both adult organisms and of eggs. Below a certain point the organization of the protoplasm cannot take place, and it is this result that shows, I think, that we cannot look upon the whole as simply the sum total of similar parts, but as itself having a single plan of organization or structure.

If we next proceed to an examination of the method of development of pieces of older embryos we find some further facts that bear on our problem. It has been found that if the hollow blastula of the sea-urchin be cut in two, the opening in

[1] The form of the new part must also be a factor in the problem, for the same amount of material, if of a different shape, might give rise to more or less rings. The part of the body from which the new substance arises may be still another factor.

each piece soon closes, and a new sphere of smaller size forms from each piece. These spheres then proceed to pass through the later stages of development characteristic of the sea-urchin development. Driesch has found that if the embryo is cut in two at a later stage, when the process of gastrulation has begun, not only the piece that contains the part about to invaginate will continue to develop and produce a whole embryo, but the piece from the opposite side will also form a gastrula and embryo. If, however, the same experiment is carried out after the gastrulation has been finished, these pieces of the outer wall fail to produce a new gastrula. A similar result was obtained in still later stages in regard to the formation of the two pouches that pinch off from the inner end of the archenteron of the starfish embryo. If the inner end of the archenteron is cut off before the two pouches have formed there, they will be formed again from any part of the more proximal portion of the archenteron; but if we wait until the pouches have once been completely formed by the archenteron, and then cut off the inner end of the latter, the two pouches are not made anew at the cut-end. In other words, after the archenteron has once produced the two pouches it seems to lose *throughout* its entire length the power of repeating the process, although at an earlier stage all the parts possessed this power.

Another somewhat similar result has been recently obtained by Spemann. If a thread be tied around the middle of the embryo of the frog at the time when the medullary folds are appearing, the egg being partially constricted by the thread into a more anterior and a more posterior part, the latter will produce at its anterior end (where the string constricts the nerve plate) a new head, and there is produced in this way a double embryo with two heads, one at the anterior end, and one behind this at the middle where the constriction is present. The result shows that the material of the dorsal nerve plate is totipotent in so far as the formation of all the structures of the brain, eyes, and nerve cord are concerned, and that the position of any part in relation to the rest determines its differentiation. The brain forms at the anterior end of the nerve-plate, but it

may also appear in the middle of the plate if the middle comes to represent the anterior end, as is the case in the experiment just described.

A most important theoretical question is involved in these results, although it has not been as yet sufficiently considered by those who have carried out the experiments, *viz.*, that a stage once passed through by the embryo cannot be repeated again by the other parts of the body that may not have been directly concerned in the operation, although these parts possessed this power at an earlier stage. A thorough discussion of this important question would lead us too far from our present subject, but I may point out that the result indicates that at each stage in the development the ultimate structure seems to change its organization, so that it no longer repeats a stage once completed. The organism has not, however, lost the power of forming a new individual, or at least certain parts have not, since eggs are produced by the adult animal, each of which may make an entire organism, and the adult animal has also the power in many cases of replacing lost parts, although it does not repeat the embryonic processes in doing so.

When we examine the method of development of pieces of still later stages of the embryo we find the process more and more like that which takes place in the adult. In the higher forms (echinoderms, mollusks, annelids, and vertebrates) the regeneration of the late stages of the embryo, or larvæ, and of the adult takes place by the development of new material at the free end, while in the earlier stages in certain embryos in these groups a new whole is established by the entire structure changing over into the new form. In other words, the method of development of pieces of the early embryo is like that followed by the lower animals, *i.e.*, by a process of morphallaxis, while in the later stages of development the method of regeneration is more like that in the higher animals. The difference seems to be connected with what we call the specialization of the tissues in the later stages of development and in the adults of the higher forms, but what is meant by this specialization is a question that needs to be further examined, although it will not be possible to do so at the present time.

We have seen that there is both for pieces of the adult animal and for pieces of the egg, or of the isolated blastomeres, a lower limit of size below which a piece does not produce the typical form. Even in a form like Tubularia, in which a very small piece may produce an incomplete structure, there is still a lower limit below which the pieces do not produce any structure. We find this lack of power to develop in small pieces in which we know from other experiments that the material is totipotent, and the only clue we have to account for the facts is that the result is in some way directly connected with the *amount* of material present. We find for each animal a lower limit of size — a limit that may vary at different stages of development — for producing a miniature copy of the type form; or, in other words, the organization must have a certain amount of material in order to develop. We find this same law to hold for pieces of eggs, of embryos, and of adult Metazoa, and it is equally true for adult unicellular Protozoa. It has been found that very small pieces of the egg may continue to divide, although they may be much too small to produce an embryo; but as several other results have also indicated, the factors that determine the cleavage are not necessarily connected with those that relate to the organization of the embryo. Isolated blastomeres that are below a certain size also fail to produce an embryo. The one-eighth blastomeres and even the one-sixteenth blastomeres produce in some few cases the early stages of development, but many of them fail to do so, and beyond this point it is doubtful if a blastomere can develop past the gastrula stage. The results show that the lower limit is soon reached in these eggs. It is certain that for adult animals pieces much smaller than one-eighth or one-sixteenth of the body can produce new animals of half size, but we have at present no data for comparison between the absolute minimal size of a piece of the egg and of the adult of the same species that can produce a whole animal. It has been found that pieces of planarians that contain less than $\frac{1}{100}$ of the volume of the adult may produce the typical form. Pieces of hydra $\frac{1}{200}$ of the adult produce a new hydra; and pieces of the stem of Tubularia about $\frac{1}{245}$ of the length of the stem can also make

a new hydranth and stem.[1] The eggs produced by these forms are much smaller — hydra perhaps is to be excepted — than these minimal-sized pieces, and as the egg produces the typical form we cannot expect to find any agreement between the ultimate size of an isolated blastomere and of a piece of the adult that produces a whole structure.

Peebles found that a smaller piece of a young bud than of the wall of hydra would produce a whole organism. The result is interesting inasmuch as the region where the bud appears is also a part of the wall. We find in a growing region of this sort that the protoplasm is denser than elsewhere, and may contain at first less water than other parts of the body, so that the absolute amount of living substance may be the same in a small piece of such a bud as is contained only in a much larger piece of the wall elsewhere. If this is true, and if the egg can also be shown to contain relatively less water in its structure than do other parts of the adult animal, it may still be possible that the amount of living substance necessary to give rise to the typical form may be found to be the same in the piece of the egg and of the adult. At present, however, we lack the data necessary to make the comparison. It is certain that in many forms — as for instance in the starfish — a piece of the adult that can regenerate the entire structure must be at least several thousand, perhaps million, times greater than the egg and must contain a much vaster amount of living substance. Many other factors than that of mere size must come into play in such cases, and it seems to me that the comparison is not, after all, of much theoretical importance, since the method of development of a piece of an egg and of an adult may be entirely different.

[1] The length of the stem is so variable in Tubularia that a comparison is difficult. If we assume the length of the stem to be 35 mm., then a piece of the stem measuring $\frac{1}{7}$ mm. in length is about $\frac{1}{245}$ of the whole; and pieces of this size produced a new hydranth and stem.

II.

A year ago[1] I reviewed the different hypotheses that have been advanced to account for the phenomena of regeneration and I pointed out that if the development of a part of an egg, or of an embryo, is also a process of regeneration, as I believe to be the case, the same hypotheses ought to apply also to the development of these parts. It may be, therefore, worth while to see how far these hypotheses may account for the development of pieces of the egg or embryo.

Bonnet extended his theory of præformed germs, primarily invented to explain the development of the embryo from the egg, to include the phenomena of regeneration. At that time the development of a part of an egg was not known, but there is no obstacle at present to applying the same interpretation to the development or regeneration of parts of the egg and embryo. In fact, Weismann, who also believes in a theory of præformation both for egg-development and for development of pieces of adult organisms, has applied the same view to the development of parts of an egg. The theory of præformed germs as held during the seventeenth and eighteenth centuries need no longer be seriously discussed in the form in which it was then expressed, since we have abundant evidence to disprove the view; but the same conception has appeared again in a more insidious form in our own time, and has been applied not only to development of the egg, but also to the regeneration of both the adult and embryo. I shall not attempt to repeat here the arguments in favor of or against this view, but shall confine what I have to say to those points that bear on our present examination. The modern form of the doctrine of præformation as held by Weismann and his school is as follows. There exists in the nucleus of the egg præformed germs that correspond part for part to the later structures that develop from the egg. The process of development is a process of sorting out of the nuclear germs to different parts of the embryo, and later, by the action of the germs contained in each nucleus on the protoplasm of each cell, they

[1] Woods Hole Lectures, 1899.

determine the differentiation of the cell. In other words, the protoplasm is looked upon as a kind of indifferent medium on which the nuclear germs feed and multiply, and, replacing the protoplasm of each cell, produce there their particular product.

In order to account for the regeneration of parts of the adult it is assumed that there has taken place during development not only an unraveling of the qualities of one germ, but at the same time at each or many of the divisions of the nucleus a quantitative division of another original whole germ, or later of a part of that germ, into like parts. This second germ is a sort of reserve stuff for future contingencies, and during regeneration this reserve stuff is supposed to become active and to do what is required of it. Pieces of the egg or of the embryo are also supposed to be able to regenerate, owing to the presence of this *reserve idioplasm* or germ in each nucleus, that is awakened into activity by the injury to the whole and then proceeds by qualitative division *of exactly the right sort* to set free the necessary germs to complete the embryo.

I need not repeat here the many objections that have been brought forward in opposition to Weismann's view, or stop to point out how the upholders of this view have been obliged again and again to add subsidiary hypotheses to meet the objections that have appeared, but I may indicate at least some of the difficulties that this view meets with from the point of view of regeneration in the egg and embryo.

The hypothesis assumes that at each division of the egg a sorting out of the qualities of the embryo takes place. Observation shows, however, that at each division there is an equal division of the chromatin, and not an unequal division, as would necessarily take place in some of the divisions, if the hypothesis is correct. The experiments with the ctenophore egg indicate that the protoplasm is an important factor in the early divisions. The experiment of compressing the frog's egg during its period of division, so that a distribution of the nuclei in the protoplasm, different from that in the normal egg, is brought about, indicates that the early nuclei are equivalent; and the development into whole embryos of pieces of the egg in which

the segmentation nucleus passes through fewer divisions than in the whole egg also points in the same direction.

The regeneration of pieces of Hydra, Tubularia, and Planaria shows that at every level of the body the cells have the power of producing any part of the organism,[1] and we must regard them as totipotent, or nearly so. The same conclusion is arrived at from a study of the development of isolated blastomeres. These facts, and others that might be given, furnish, I think, a strong argument against Weismann's hypothesis, and I believe we must look in a different direction for a solution of the problem of development and of regeneration.

We should be careful to distinguish between the idea of predetermination and that of præformation. The former includes the latter, but also much more, and is, in fact, an almost necessary idea in connection with the phenomenon of development, at least in one sense. Every egg of the sea-urchin is predetermined to give rise to a sea-urchin *so long as the conditions remain as we find them at present*, but it by no means follows that the hypothesis of *præformation* is a necessary consequence of this view. It is true that since each egg passes through the same stages to reach the same goal we must regard the series of changes as predetermined in the structure or composition of the egg, and in the external conditions surrounding the egg, but the way in which the development takes place may be in no way connected with the presence of a præformed germ of the embryo or with the presence of præformed germs of any sort in the nucleus. In fact, a process of pure epigenetic development, as generally understood nowadays, may also be predetermined in the egg. It is well, I think, to be clear on this point, since otherwise we grant too readily the necessity of assuming some sort of præformation hypothesis.

In my Woods Hole lecture of last year I considered the hypothesis of formative stuffs and reached the conclusion that it is insufficient to explain many of the phenomena of regeneration. Let us see if this view will apply to the development of parts of the egg and embryo. In the first place, it should be noticed that the hypothesis was primarily invented to account

[1] At least so far as the different layers are concerned.

for those kinds of regeneration in which a new part is added at the end of the old part, and, as I have pointed out, it is not well suited to explain those cases in which a piece changes over entirely into a new whole. Since the development of parts of the egg and of isolated blastomeres and pieces of the embryo takes place by a process of morphallaxis, it is clear that the hypothesis is equally inapplicable to such cases. The kind of rearrangement or regulation that takes place in a piece of an egg, or of an isolated blastomere, or of a piece of a protozoön, so that a symmetrical whole is formed, cannot be made any clearer, I think, by the assumption of specific fluids or stuffs in the different regions that determine the later differentiation.

The idea that there is a similarity between the process by which a broken crystal completes itself and that by which an animal or a plant may make good a lost part has often been suggested. The comparison rests, I think, on a superficial resemblance, and a careful examination of the nature of the two processes shows them to be the outcome of different factors. It may, however, be asked in what respects is the modern view of crystallization different from the view which I have advocated in regard to the reorganization of the protoplasm in a part of an egg or in a piece of hydra. The two conceptions are in reality entirely different. A piece of a crystal does not rearrange its parts, much less its axes, to form a new whole of smaller size, but has deposited on its surface, from the saturated solution in which it lies, new material that conforms in every respect to the original axes and planes. In a piece of an egg or of an animal, on the contrary, the entire old structure changes over into a new whole involving in some cases a change of axes.

Pflüger's conception of the process of regeneration has many points of resemblance to the idea of the recompletion of a crystal. He applies the conception, however, only to those cases in which the regeneration is by a process of addition to the old part (epimorphosis). Pflüger's hypothesis is that at the cut-end the old material attracts from the blood new material, which is deposited over the cut-surface and is there organized at its region of contact with the old part. He speaks of the new molecules being organized at the region of contact with the

new ones, and those that have thus been organized are supposed to attract others which are then deposited on the outer end and in turn become living structures. This idea is not fundamentally different from that held at present as to the growth of a crystal, except in so far as the molecules are supposed to be organized by those in the old part or by those that have previously been altered, etc. But on this view we have no explanation of the process of morphallaxis, for, in this case, the change takes place only in the old part and throughout the old part. If we attempt to extend Pflüger's idea so that it may include these phenomena, we must suppose that a sort of recrystallization takes place in the old tissue or isolated piece; but this is really a very different conception from the former, for the process is not reorganization by apposition, but by complete working over of the entire piece into a new whole. This idea is entirely foreign to our conception of crystal growth, and also to the conception entertained by Pflüger. I have also pointed out that even in some cases in which a new part is added to the old one there are grave difficulties in the way of accepting Pflüger's view, especially in the case of the planarian, in which the new head does not appear in the middle of an anterior oblique exposed edge, but to one side of the middle line, where the influence of the old part would produce, on Pflüger's view, a very different result.

Finally, I wish to discuss a problem that is at present one of the most difficult questions in connection with the process of regeneration. I mean our idea of polarity or polarization of the living material of the animal and plant. The term was first used by Allman in 1864 to mean that a new anterior end appears on that part of a piece that lay nearest to the old anterior end, and a posterior end appears on that part that lay nearest the old posterior end. This rule is followed in a great many cases, but it is not invariable. In certain forms an organ different in kind from the one removed has been found to develop. The first case of the kind was described by Bonnet, who found when certain fresh-water worms were cut in two that the posterior piece produced at its anterior end, not a new head, but another new tail. Loeb also has described

several other instances of the same phenomenon in hydroids, and has made the additional and important discovery that in these forms the external conditions may determine the kind of regeneration that takes place. However, even in these forms differences are present in the two ends of a piece, for, even in the most favorable forms it is found that, as a rule, a new head or hydranth forms sooner on the anterior end of the piece than on the posterior, and from the posterior end of the piece a posterior end is more easily developed than from the anterior end. In other and higher forms the factors that determine the kind of regeneration seem to come from within the piece itself. In some of these forms we also find occasionally that the new part may be different from the part removed (heteromorphosis), and in some cases, as in Bonnet's fresh-water worm, a posterior end develops on an anterior surface. Other cases of the same sort are also known; for instance, in the earthworm, Allolobophora, a short posterior piece (less than half the length of the worm) generally produces at its anterior end another tail; a very short piece of the head-end may produce a new head on its posterior surface, and the same holds for short pieces of the head of a planarian.[1]

Sachs has vigorously combated this idea of polarity, that he refers to as a metaphysical notion of the morphologists, and offers as a substitute his hypotheses of formative stuffs. I have attempted to show that the idea of formative stuffs is insufficient to explain the phenomena of regeneration, and at present I see no escape from the idea of a polarity of some sort existing in the organism. On the other hand, we cannot be too careful in clearly defining what we intend to include in this idea of polarity, for I think we can see even at present that we must form a conception of the polarity different from that in which the term is used by the physicist.

The term "polarity" when used in connection with phenomena connected with the magnet means that there is a difference in the two ends of the magnet. The idea also involves the further one that any piece of the magnet also shows this same

[1] We may call that kind of heteromorphosis in which the new part is more or less a mirror figure of the old part "amphimorphosis."

difference at the ends, and since this is found to be true for every smallest piece of the magnet, it is assumed to be a property of each molecule or atom of which the magnet is made up—the magnet being the sum total of the action of all its molecules. We speak also of a crystal showing polarity in the sense that it has a definite form that can be referred to definite *poles* and *axes*, and it is supposed that this same property is possessed by the smallest "crystal molecules" of which the crystal is made.

On the other hand, in an animal or in a plant in which we find the two ends of a piece behaving differently, yet always showing the same constant difference, although we have a result resembling in many respects the polarity of the magnet, we find also in several essential respects differences and, I think, fundamental differences (in the sense that they are the outcome of different factors) between this phenomenon and that in the magnet. For instance, we find in the pieces of Tubularia that external conditions may reverse entirely, after a time, the polarity of the piece, so that a head may appear on the posterior end even while another head is present on the other end. We know of nothing similar in the case of the magnet, unless we consider the change that can be brought about in it by re-magnetization; but there are quite obvious differences in the two results. The most fundamental difference, however, between the two conceptions is, I believe, connected with the kind of structure that we must suppose to be present in the two cases. The polarization of the magnet is the sum total of a vast number of smaller units, each unit being itself a magnet. On the other hand, we have at present clear evidence to show that while the polarity of the organism is the outcome of its structure or organization, this is not the effect of the presence of a large number of units of which the organization is only the sum total, but, on the contrary, the organism is itself the ultimate unit that makes the polarity, and while we must believe that this same organization may develop in a piece of the original whole, the evidence goes to show that the reorganization is of a different nature from that by which a piece of a magnet becomes *at once* a new magnet.

In the first part of this paper I have given my reasons for looking upon the organization of living things as a phenomenon *sui generis*, and I have wished to bring here into connection with this consideration the conception of polarity as applied to the organism. It is a phenomenon, I think, that is different from the one bearing the same name applied to inorganic substances. We are therefore, I think, justified in looking upon the reorganization of pieces of the egg, embryo, and adult as a phenomenon peculiar to the living structure of the egg, and without a parallel in inorganic nature. It seems to be one of the peculiar physical properties connected with the matter that we call living substance, and in the last analysis we find it to be not simply the outcome of a complex of known physical principles. We are therefore, I believe, also justified in calling the organization of living things a vital property in the sense, to repeat what I have just said, that it is peculiar to this kind of substance or structure, and not the result of a complex of known physical principles; or, in other words, it is a physical phenomenon as fundamental as the polarity shown by crystals or the magnetism of the magnet, and just as the latter are associated with certain kinds of matter, so is the organization associated with the substance protoplasm.

THE HABITS AND NATURAL HISTORY OF STICHOSTEMMA.

C. M. CHILD.

A SMALL fresh-water nemertean, undoubtedly *Stichostemma asensoriatum* Montgomery ('96), is found very abundantly in one of the park lagoons in Chicago.

The animal has proved to be a favorable form for experimental study, and in the course of such work during the past two years a number of observations upon its habits and natural history have been made. These observations are given here in the belief that a connected account of the natural history of a single form is of value because it brings together a series of facts which, though important, often receive only incidental attention in connection with other work, or are ignored altogether, and because it affords a basis for further study.

Montgomery ('96) has given a brief description of a new American species of fresh-water nemertean which he called *Stichostemma asensoriatum*. He regards Silliman's *Tetrastemma aquarum dulcium* ('85) as insufficiently characterized, but believes that it may be closely allied to *S. asensoriatum*. The species which forms the subject of this paper agrees with Montgomery's description of *S. asensoriatum* in all respects except that it is not protandric, while Montgomery believes *S. asensoriatum* to be protandric like *S. eilhardi*. Böhmig ('98) has accepted Montgomery's genus Stichostemma for his species *S. græcense*, but as *S. græcense* is not protandric, Böhmig holds that the existence of protandry should not be regarded as a characteristic of the genus. In a personal communication very kindly made in answer to an inquiry of my own, Dr. Montgomery expresses himself as of the opinion that the presence or absence of protandric hermaphroditism is a point of minor importance. The revised genus diagnosis of Stichostemma as given by Böhmig ('98) is as follows:

"Augenzahl veränderlich, gewöhnlich mehr als 4; 9 oder 10 Rüsselnerven; das Rhyncocoelom erstreckt sich nicht bis an das Körperende; die Nephridien dehnen sich von der Gegend des Gehirns bis zur hinteren Körperspitze aus; zwitterig, ovipar." The species found in the vicinity of Chicago agrees with *S. græcense* in not being protandric, but since I cannot find that it differs in other respects from the description given by Montgomery of *S. asensoriatum*, I am inclined for the present to regard the two as identical. It appears probable, moreover, that *S. asensoriatum* Montgomery is identical with *Tetrastemma aquarum dulcium* Silliman. In any case the two forms are closely allied, as Montgomery admits.

The species under consideration is a slender worm, attaining often a length of 20 mm. (Montgomery gives the maximum length as 18 mm.). It varies in color from a light yellowish, almost cream-color, in the smaller specimens, to a deep orange-red in many of the large individuals. Even in the most brilliantly colored specimens, however, the terminal regions of the body are more yellowish than other parts. The reddish coloration is especially distinct in the nervous system. In many of the larger specimens the region of the brain can be distinguished by the naked eye on account of its deeper coloring. Individuals in which the eggs are nearly ripe show scarcely a trace of the reddish tint, being almost pure yellow in color. Animals kept in the laboratory for a long time without food usually become more or less brownish, owing to the appearance of black pigment in the integument. This pigment is occasionally found in newly captured specimens. I am inclined to believe that its appearance is connected in some manner with the lack of food.

The usual number of eyes is six, the anterior pair being the largest and the posterior pair the smallest. Variation in the number of eyes, or at least in the number of pigment spots, is of frequent occurrence. Specimens with only four eyes sometimes occur, but are rare. In case eight symmetrically placed eyes are present, the anterior pair is usually small and situated a short distance in front of the largest pair. The eyes are very often unsymmetrically placed or differ in number

on the two sides of the head. Variation in the number of pigment spots can often be observed in a single individual. One or more of the spots may divide, or in some cases a number of small masses of pigment appear in place of a single pigment spot, in consequence of a kind of fragmentation. One of these smaller masses may increase to the size of the whole, while the others disappear. Migration of these masses is often observed. A more complete account of these observations is reserved for a future time.

The body of the worm is very transparent. The alimentary canal, blood vessels, terminal nephridial organs, nervous system, gonads, the rhyncocœl, and the proboscis, with principal and accessory stilets, can be clearly seen in the living animal under slight pressure. For some time past I have employed the form for class work on account of the ease with which its internal anatomy can be studied.

The points of difference between this form and *S. eilhardi* as given by Montgomery ('96) are as follows: (1) The absence of the supraoral sense pit, which suggested the specific name "asensoriatum." (2) The cephalic gland is not as voluminous as in *S. eilhardi*, and has not one main efferent duct, but the ducts of the individual gland cells penetrate the body epithelium independently of one another, in the manner of subcuticular gland cells; the external openings of these cells lie at the anterior end of the head. The want of a main efferent duct, formed by the fusion of the individual cell ducts, might be explained by the absence of the supraoral sense pit, since in most metanemerteans the main duct discharges at the base of this pit. (3) The pigment of the body epithelium occurs exclusively in the supporting cells and is not found at all in the interstitial tissue. (4) Those gland cells corresponding to what I have termed "gland cells 3" in *S. eilhardi* are not egg-shaped, as in that species, but have an elongated narrow form; in structure and in their color reaction to stains they show a close similarity to the cells of the cephalic gland: thus, they stain intensely with hæmatoxylin, and with the triple stain of Flemming (safranin, gentian violet, orange G) combine with the safranin and not with the violet. (5) The

stilet basis is slightly constricted medially. (6) There are ten instead of nine longitudinal nerves in the proboscis.

These differences do not concern the general appearance, so that the figure of *S. eilhardi* given by Montgomery ('95, Taf. VIII, Fig. 17) might serve equally well as a general diagram of the structure of *S. asensoriatum*.

OCCURRENCE AND DISTRIBUTION.

During the early autumn of 1899 Stichostemma was found in great abundance in one of the lagoons in Jackson Park, Chicago, which has free communication with Lake Michigan. Since that time it has been present in the lagoon at all seasons of the year. Large numbers are found in masses of Spirogyra or other filamentous algæ, and often, though less commonly, the animals are found among Elodea. They are most numerous along the shore where the water is only a few inches deep. Their presence here is probably due to the higher temperature of the shallow water near the shore and the consequent more luxuriant growth of the vegetation which they frequent. Their food, which consists of species of Nais, is very abundant in the lagoon under the same conditions, and probably also, directly or indirectly, constitutes a factor in the local distribution.

The distribution about the lagoon is rather irregular and uneven. In some spots the worms are so abundant that hundreds may be taken from a single liter of the aquatic vegetation. In other spots, apparently equally well suited to these forms, only a few individuals or none at all are found. While these areas are rather definite during a single season, the worms do not always reappear in the same spot in succeeding years. It is usually necessary to hunt for the favorable localities anew each year.

The seasonal distribution is very definite. During the later summer and autumn the animals are usually very abundant, young and old together. They do not disappear from along the banks until actual freezing occurs. When the ice forms, many of the worms are undoubtedly destroyed, though a large

number of them must reach deeper water, where they continue to live beneath the ice during the winter. The lagoon is twelve to fifteen feet deep in many places, and no freezing occurs in the deeper parts. There is no evidence that the worms are capable of enduring actual freezing. After the first appearance of ice in the lagoon I have chopped out and thawed masses of the vegetation in which the worms had been abundant a few days before, but which were frozen solidly into the ice when removed. In aquaria and jars prepared from these no worms ever appeared. During the winter of 1899–1900 a part of the lagoon remained open until about the middle of January, although the weather was cold and the remainder was covered with several inches of ice. Up to this time the worms were found here in abundance. Later this area was covered with ice a foot or more in thickness, and the bottom was also frozen in the shallower parts, and at this time no worms were obtained from the region.

It is possible that the worms burrow into the mud, but samples of the mud taken at various times during the winter have never yielded a specimen. I have been unable to examine fully the deepest parts of the lagoon, but believe that the animals remain more or less active there during even the colder months.

The worms reappear near the shore in large numbers very soon after the ice begins to melt. In 1900 the lagoon was covered with from twelve to sixteen inches of ice on March 20. By March 26 the ice had melted along the shores, leaving some two or three feet of open water from six inches to a foot in depth. At this time large numbers of worms were found in this open area, nearly all of them large specimens with well-developed eggs, whereas the worms taken in January are of various sizes and mostly with very small eggs or none at all. The small worms taken in January are the young of the preceding autumn which have not attained full size. If the worms had remained inactive until the ice melted, it is difficult to understand how their increase in size and the growth of the eggs could have occurred in so short a time as three or four days. I believe, therefore, that they must have spent the month of February and the early part of March in the

deeper parts of the lagoon, reappearing at once near the surface as the temperature of the water began to rise. The small naids which form their food can be taken at all times through the winter from beneath the ice, so that so far as food is concerned Stichostemma is well supplied during the winter months.

Apparently, then, the young of the preceding autumn reach their full size during the winter, reappearing near the surface with nearly ripe eggs as soon as the ice disappears.

During the winter of 1900–1901 the lagoon was wholly covered with six to eight inches of ice before the end of December, and the temperature during the greater part of January and practically the whole of February was far below 32°. The ice became exceptionally thick and did not disappear till near the end of March. The worms were not found along the shore until April 12, and then only a few appeared, all of them large and filled with eggs which were about half grown. During the early part of December, 1900, before the lagoon was completely frozen over, the worms were more abundant than I had ever found them before. Their late appearance and small numbers in April, 1901, must probably be attributed to the protracted cold weather and the thickness of the ice in the lagoon.

During the months of May and June comparatively few full-grown specimens are found, but the young are increasingly abundant as the season advances. These become sexual about July 1 or a little earlier. By this time nearly all the old worms which survived the winter have disappeared. During the remainder of the summer the worms continue to increase in numbers until freezing kills them or drives them to deeper water.

There is no evidence that the worms possess the power of entering upon a resting stage of any kind which is capable of enduring freezing without injury, though there are some facts that indicate the possibility that they may become more or less quiescent for a short time. When the animal is brought under conditions which are disagreeable to it, or is irritated, it secretes a large amount of slime and in many cases becomes enclosed in a covering of slime, which gradually contracts and becomes more dense until it resembles a cyst. Within this the worm

may remain for some weeks, either moving slowly or not at all, or it may leave in a few days. Left in jars of clear water without algæ, the animals are likely to make these slime coverings repeatedly. As will appear below, I believe that the fact that the animal is disinclined to leave the slime is a thigmotactic reaction. Violent stimulation will often induce removal, or the slime may be picked apart with needles, thus freeing the animal, which is active and normal in appearance in every respect. In many cases mutilated specimens or animals in impure water form these coverings and remain in them until death.

It is possible that the worms may form these "cysts" about themselves during the winter. These do not, however, enable them to resist freezing and do not serve as a protection against desiccation, as will appear below. It is difficult to understand how the animal is better protected within this "cyst," except, perhaps, as regards predatory enemies, than it is under the usual conditions. While this process is perhaps to be regarded as showing the manner in which the process of encystment may arise, I think it is certain that in its present development this slime covering is of little value as a cyst. The causes and method of its formation are discussed below.

Movements.

Locomotion forward is accomplished principally by means of the cilia with which the body is covered. During the forward movement the head is turned slightly from side to side in regular succession, and as the body follows the same course the movement as a whole is distinctly sinuous, the body showing altogether four or five curves to left and right at any given time. It is probable that under normal conditions the sinuous character of the movement is a distinct aid in locomotion. In crawling through masses of algæ the lateral movements of the head will, of course, enable the animal to find the interstices more readily, while the sinuous bending of the body affords a firmer support and a greater power for forcing a way among the tangled threads. The value of these movements in enlarging

the field of direct stimulation and contact is evident. The animal crawls along the bottom of a jar with the ventral surface uppermost almost as often as in the other position. It is unable to support itself free in the water, although it often drops from the surface to the bottom, making the usual crawling movements during the descent. During all forward movement the head is continually making rapid searching movements in all directions.

Backward movement is accomplished in a manner entirely different from that just described for forward locomotion, *viz.*, by muscular contractions.

The muscular activities concerned in backward locomotion consist of a series of peristaltic waves. A contraction of the circular muscles near the posterior end occurs, and the end is thrust backward; then a wave, consisting of strong contractions of the longitudinal and relaxation of the transverse muscles, producing a shortening and thickening of the region affected, begins at the posterior end of the body and travels forward. The whole process is quickly repeated, and in continued backward movements three or four of these peristaltic waves may be visible on the body at one time. On a smooth surface like glass these movements are rather ineffective, but it is easy to see how, under natural conditions, the posterior end of the body becomes more or less completely fixed as soon as increase in size begins and the other portions are drawn back to it.

The body is extremely contractile, and different parts are capable of independent contraction. In the reassumption of the extended position after contraction, the extension usually begins at the anterior end and proceeds backward along the body as the head advances.

Movements of the proboscis within the rhyncocœl are very common. Contraction of the circular muscles in the posterior portions of the body causes the proboscis to be thrown forward, and, conversely, extension of the head region forces it backward. In general the proboscis, together with the fluid of the rhyncocœl, tends to occupy the region of least pressure.

The relation of the cilia to the different movements is interesting. During forward movement the cilia are in active

motion and constitute the chief organs of locomotion. If, however, the forward movement ceases suddenly, or if the head be slightly drawn back, the cilia in the part affected stop their movement and remain nearly perpendicular to the body surface. If the animal remains quiet for a short time the cilia may begin to move slightly. It is difficult to determine whether this movement affords any definite impulse in either direction, but observation indicates that there is a very slight backward current along the body. When the head and anterior portions of the body are suddenly and violently drawn backward, as often occurs, or if the animal begins to move backward, the cilia of the contracting region are laid flat against the body, all pointing forward, and resume their usual position when the backward motion ceases. The body is at all times covered with a thin layer of slime, and it is possible that the turning forward of the cilia may be simply the result of the backward movement of the body through the slime. Observation of the head region, which is constantly undergoing contraction and extension, shows a beautiful play of the cilia, and often in the rapid but very slight contractions without actual backward movement, the cilia over a considerable area are all instantaneously turned forward against the body, perhaps to reappear almost immediately. The rapidity and uniformity of their change of position render it probable that it is the result of a definite stimulation similar to that causing reversal of the cilia in many other forms.

I have not been able to find any indications of actual reversed beating of the cilia causing backward movement of the body. The backward movement is apparently brought about wholly by muscular contractions, the cilia being laid against the body and pointing forward, so that they offer no resistance, but remaining motionless or making very slight indefinite vibrations. These conclusions agree well with those reached as the result of macroscopic observations on the moving animal. Stichostemma does not appear to glide backward, but accomplishes this movement by violent muscular contractions as described above. Except when the stimulation is very intense and sudden, it is more likely to turn the head

back upon the body and thus to change its direction of movement, than it is to move bodily backward.

As in other nemerteans and in turbellaria, the body is always covered with a thin layer of slime or mucus secreted by the dermal glands. Any stimulation or irritation causes an increase of this secretion to such an extent that the animal becomes enveloped in a thick layer of the substance. The animal is able, like many other related forms, to move beneath the surface film, and presumably this secretion is an important factor in locomotion here and elsewhere.

Small dishes in which a number of specimens are kept become filled with long strands and masses of the slime, in which the animals move about. The accumulation of the secretion does not appear to injure the animals in any way. Wilson ('00) has noted the large amount of slime secreted by Cerebratulus, and his observations are paralleled by my own. Certainly for so small a form as Stichostemma the amount of this slime secreted is extremely large.

RESPIRATION.

Respiration undoubtedly occurs through the surface of the body. The swallowing of water which Wilson ('00) has observed in Cerebratulus has never been seen in Stichostemma. The animals are apparently sensitive to changes in the oxygen content of the water, but their small size and the absence of a cuticle probably render special respiratory organs unnecessary.

FOOD.

The only food which the animal is known to take consists of specimens of Nais which are captured and gradually drawn into the alimentary canal. The actual capture of these animals has never been observed, although in several cases they have been seen in the partially digested condition in the alimentary canal, and in one case a specimen was found with a large Nais partly swallowed. The Nais was as long as its captor, and although half its body was in the alimentary canal of the

nemertean the free portion made active movements. The nemertean was comparatively quiet, but at short intervals the mouth was widely opened and the body extended, and in this manner the Nais was drawn further into the alimentary canal. It could be clearly seen through the body wall of the nemertean that digestion of the annelid was proceeding very rapidly. Later a part of the Nais was disgorged, and some portions were seen to be completely disintegrated, while others which had been in the alimentary canal only a few minutes, ten to fifteen, showed distinct evidences of digestion. This rapid digestion of the food was also observed by Wilson ('00) in the case of Cerebratulus.

It appears extremely probable that the food is captured in the manner which Wilson ('00) has described for Cerebratulus, though I have never observed it. Indeed, there is a striking similarity between this form and Cerebratulus, both in the nature of the food and in the method of taking it. In the cases of both an actively moving annelid forms the food, being attacked and overpowered by the nemertean, and in both cases the prey is often as large as its captor and always more active. I have not been able to determine whether Stichostemma always begins the process of swallowing at the posterior end of the body of its prey. In the one case of feeding actually observed, the head of the naid had been broken off completely and lay in the slime secreted by the nemertean, but the free end of the annelid was apparently the anterior end from which the head had been broken. In the bodies of the naids which had been completely swallowed digestion had always proceeded so far that it was impossible to determine with certainty which was the anterior end.

The feeding apparently takes place only in darkness, or in light of little intensity, and therefore occurs normally during the night. During the day the nemerteans may remain in direct contact with the naids in the interstices of the masses of algæ, but apparently do not attack them. The next day, however, or after a few hours in darkness, the naids are fewer in numbers and the intestines of the nemerteans indicate very distinctly a recent meal. The failure to observe the actual capture and, in all but the one case mentioned above,

the swallowing of the food, is probably due to the fact that the nemerteans are easily disturbed by a jar or movement of the dish containing them, and especially by the light. In such cases they probably release the prey or disgorge it, if partly swallowed, as in the case described above.

There is no direct evidence that the adult animal takes other food under normal conditions. The fæces, so far as recognizable as such, always contained the setæ of naids. Moreover, specimens have been kept for weeks in jars with many other animal forms, Protozoa, Turbellaria, rotifers, copepods, ostracods, etc., but no traces of any of these forms have ever been found in the alimentary canal.

The nature of the food of the young individuals is a matter of interest. When first hatched they are less than a millimeter in length. Probably they do not take food immediately, but they certainly feed when from one to two millimeters in length. The food at this time probably does not consist of naids, for it is difficult to understand how these small animals could capture any except the very smallest. I am inclined to believe that they feed upon other small forms during these early stages, though I have no direct evidence upon this point.

I have often suspected the animals of eating each other. In jars containing a large number of specimens there is always a remarkable decrease in numbers during the first weeks, and the walls and bottom of the jar do not show the whitish disintegrating masses that are always found, even after several days, in dishes where isolated specimens die. Moreover, it is the smaller animals that disappear, those remaining being of large size and appearing well fed. I think the circumstantial evidence in favor of the view that the worms readily devour members of their own species is very strong, but here again I have not been able to make actual observations.

The animals are capable of living for a long time without food. Single specimens have been kept for more than three months in jars of clear water with no other life except probably a very few Protozoa. In one case a jar containing a number of individuals was kept for six months. Three of the animals survived during this time.

During starvation a great reduction in size occurs. During the earlier stages the animal grows somewhat more slender, but later its length is also greatly reduced. In the case mentioned in the preceding paragraph the three specimens found at the end of the six months were less than five millimeters in length, though of about the normal proportions. When placed in the jar the specimens were of average size, *i.e.*, from twelve to fifteen millimeters in length. The reduction in size was wholly due to lack of food.

The starving forms usually acquired after a few weeks a blackish pigmentation, granules of black pigment being deposited in the body wall and increasing in abundance until in some cases the body had lost its light yellowish color and become a dull, dirty brown. In such cases microscopical examination showed the whole surface of the body to be dotted with small granules of black pigment. This pigment is not altogether absent in newly captured and apparently well fed specimens, but is usually not sufficiently abundant to have any appreciable effect upon the general coloration of the body. It undoubtedly corresponds to the pigment mentioned by Montgomery ('**95**, pp. 99–100) as occurring as an interstitial tissue.

The increase in the amount of pigment is undoubtedly connected with some alteration in the metabolism. It is possible that it is not directly connected with starvation but with some other effect of captivity; but, as far as my own experience is concerned, it appears in specimens which have been without food for some time. Decapitated specimens or pieces of the body, which may live for months, sometimes become distinctly brown or blackish.

Reaction to Stimuli.

As regards the reactions of the animal to stimuli, it is not intended to give here the results of extended experimentation. Some work has been done along these lines, but the results are reserved for a later time.

PHOTOTAXIS.

The most conspicuous reaction is the reaction to light. The animal is negatively phototactic for even moderate light intensities. The response is very distinct and definite. If a number of animals in a dish or jar be brought suddenly into diffused daylight, each begins almost immediately to move in the direction away from the source of light. Within a few seconds every animal in the dish is moving in this manner. Arrived at the opposite side of the dish, the animals do not immediately come to rest, but move about restlessly, following the sides of the dish, or in some cases even turning back toward the light for a short distance. The final result of these movements in a cylindrical jar is the aggregation of the worms in the region of least light intensity, not at the point farthest from the light but on the two sides at a point midway between the points farthest from and nearest to the light, where a large part of the light is shut off by the walls of the jar. In this respect these animals resemble Planaria (Loeb, '93), with the difference, however, that they are more restless and do not form such distinct and well-marked aggregations under these conditions as does Planaria.

In jars kept in a dark closet or in diffuse daylight on dark, cloudy days or toward night, the worms crawl about freely; *i.e.*, they are not distinctly negative for very low intensities. Examination of a jar during the night shows the worms to be active. They are thus evidently nocturnal in habit like Planaria.

Animals from which the whole head, including eyes and brain, has been removed, react to light in the same manner as do normal animals, but the reactions are slower and less exact (Parker and Burnett, '00).

The question as to whether the reactions of Stichostemma are strictly speaking phototactic or photopathic, whether two different kinds of reaction occur, is perhaps not easily decided. Certainly, so far as experiments already made indicate, there is nothing in the reactions of the animals to light that cannot be explained as due to the effect of different intensities without relation to the direction of the rays (Holt and Lee, '01).

Thigmotaxis.

The thigmotactic reaction is positive and distinct. The animal shows a strong tendency to crawl into interstices and is usually found in masses of algæ. In clear water it will commonly select the angle between bottom and sides of the jar and gradually come to rest there.

Several specimens in a jar of clear water will often aggregate in a single mass, crawling over and between each other and finally becoming nearly quiet.

A single individual, when it changes its course of movement, does not commonly make a curve but turns the head directly back against its own body and retraces its course. Undoubtedly the animal reacts thigmotactically to its own body. In a similar manner on coming into contact with the body of another individual, or indeed any object, the worm crawls along its sides or edges, seeking the spots where the greatest portion of its body is in contact with surfaces.

Formation of "Cysts."

Since the formation of the cyst-like slime covering, mentioned above, appears to be more or less closely connected with the thigmotactic reactions of the animal, it is discussed a little more fully here.

As noted above, there is a considerable increase in the amount of slime secreted when the animal is irritated in any way. Any strong stimulation, *e.g.*, strong light, handling in a pipette, etc., appears to cause this increase in some degree. Animals placed in a jar of perfectly clear water without algæ or other places of concealment show a tendency to settle in accumulations of their own slime, and it appears, in some cases at least, that the secretion becomes more dense under these conditions. It often happens that within a day or two an animal becomes surrounded by a dense coat of somewhat elastic slime, which even after removal of the animal retains a more or less definite form. Within this slow movements may go on continuously. Sometimes the body is so closely

coiled that the covering is almost spherical, or the body may simply be bent back upon itself at one or two points, thus giving the covering an elongated form. The worm often remains in this covering for days or even for weeks, but may leave it at any time. That the animal is not incapable of making its way out is shown by the fact that violent stimulation will usually cause movements of sufficient force to rupture the wall of the covering and free the enclosed worm. The most interesting fact, and one which, as I believe, throws some light on the nature of this phenomenon, is that even after repeated stimulation or after rupture of the wall with needles, the animal in many cases exhibits an apparent reluctance to leave the covering. The head is protruded, makes the usual searching movements, and then is withdrawn again, and the worm continues its slow movements within the cavity of its case.

I believe that the enclosure of the animal within this secretion, and its apparent reluctance to leave its covering, are the result of the strong positive thigmotaxis which other actions show to be present. In a jar of clear water the slight accumulations of slime, which are the result either of irritation by strong stimuli or have been formed by the continuous secretion of slime at some particular spot where the animal has rested for a time, serve in some degree as a contact stimulus, and the worm tends to remain in or about them. Continued secretion leads to the formation of a more or less definite coat of slime, within which a cavity is formed by the continuous crawling of the worm. Various parts of the coiled and twisted body stimulate the sensitive head, giving the sensation of contact, and the head may often be seen to force its way in between two moving coils of the body, the whole body following. Thus the animal is constantly forming new figures and arranging its body in complex coils within the slime. From time to time, if the animal is well fed, the fæces and intestinal mucus are added to the wall, which thus becomes whitish and more opaque. Within the covering, then, the impulse which leads the animal to seek contact with surfaces is satisfied, and a strong stimulus is necessary in order to induce emergence. This latter fact

is clearly evident from the apparent reluctance noted above to leaving the covering, even after violent stimulation. The head being protruded finds no contact surfaces except the flat glass, and is again withdrawn. In some cases worms which had been removed from the mucous coverings happened to come into contact with the latter again in their wanderings, and after crawling about over them reëntered them, thus showing in the clearest manner possible the thigmotactic nature of their preference for these cyst-like coverings.

Another interesting habit which these worms exhibit is closely related as regards its causes and nature to that just described, and is also clearly thigmotactic. In many cases, in their restless wanderings after introduction into jars of clear water, the worms reach the surface. They may crawl anywhere upon the surface film, but prefer the margins, where the surface of the water curves slightly upward toward the glass. Undoubtedly the surface tension of the water affords a certain resistance to their movements here and calls forth a contact sensation. Into this angle between the surface film and the side of the jar the worms push their way and then crawl completely out of the water and up the side of the jar. The slime secreted by the surface prevents immediate desiccation, but becomes thicker and harder as evaporation goes on, and thus in even greater degree than the slime coverings in the water affords the sensation of contact. The worms never attempt to return to the water, but remain within the cases thus formed until death ensues, which occurs within a few hours. The whole series of reactions leading to the emergence from the water and the failure to seek it again is thigmotactic.

If the animals do not leave the water within the first twenty-four hours after being placed in the clear water they very rarely do it afterward unless they are again set in active motion by some strong stimulus. I have kept worms in a jar of this kind for three months; the only specimens which left the water did so within the first day or two, although the conditions within the jar remained equally unfavorable during the whole period.

The fact that the animals tend to leave clear water only during a short time after being placed in it is undoubtedly due

to temporary excitement in consequence of handling, strong light, etc., when first introduced into the jar. For some time they are very active and many of them reach the angle between the surface of the water and the sides of the jar. Some of them force themselves into the angle with powerful movements and thus leave the water. Later the movements become less rapid, and even when they happen to reach the angle between the water and the side of the jar they content themselves with following it or remaining quietly in it. Moreover, others have meanwhile come into contact with other individuals or with slight accumulations of slime and tend to remain quiet. It is probable that there is also some degree of acclimatization to the new conditions, so that they in themselves fail after a time to stimulate the animal as strongly as they did at first.

It is clear that the formation of these coverings cannot be regarded as constituting a true encystment. The animal does not enter a quiescent stage within the covering, nor is it enabled to survive conditions which would otherwise cause death, except that its life may be lengthened for a few moments by the formation of the covering after it leaves the water, or that it may in some cases escape the attack of predatory enemies by formation of the slime covering.

The formation of the coverings is the result of the following conditions: the surface of the body is constantly secreting slime, and stimulation or irritation causes an increase in the amount of the secretion, perhaps also some change in the quality; and secondly, accumulations of this slime are of sufficient density to call forth in some degree the positive thigmotactic reaction.

On the other hand, it is quite possible, and even probable, that the process of encystment might arise in some such manner as this in a positively thigmotactic animal. Indeed, in the present case a change in the quality of the secretion, rendering it less permeable to water, appears to be the only, or at least the principal, modification necessary for the formation of a true cyst. It is possible that in Stichostemma the secretion may become so modified in time that the animal will succeed

in tiding over the dry seasons by becoming encysted, and will then become capable of living in shallow, temporary pools, which dry up during a part of the year.

At present, however, the formation of the slime coverings cannot be regarded as an adaptation to particular conditions. It is merely an incidental result of certain reactions of the animal which have no relation to lack of water. In those cases where the animal leaves the water the result is always or nearly always death. If the nature of the secretion should for any reason undergo change in some individuals or races, selection of those secreting the most impermeable covering might occur.

The question as to whether the emergence from the water ever occurs under natural conditions requires a brief consideration. It might be supposed that in nature the animals can always satisfy the thigmotactic impulse among the vegetation and débris beneath the surface ; but since the reaction is so distinct, and includes so large a proportion of the animals in clear water in the laboratory, I can scarcely believe that it does not occur sometimes in nature, and probably very often. Moreover, as is noted below, foulness of the water often induces the emergence, and in the lagoon where these worms are found the water in certain localized regions may become stagnant to a considerable degree in consequence of the decay of the luxuriant vegetation. I believe, therefore, that the animals must leave the water frequently in nature, and that these individuals are usually eliminated. It is possible that an animal which has left the water may occasionally find its way back to it, but I have never been able to observe a case of this kind in the laboratory, though I have often looked for it.

It appears probable, however, that the change from an aquatic to a terrestrial habit may be due, at least in such forms as the turbellarians and nemerteans, to a positive thigmotactic reaction which leads the animal to force itself into the angle between the surface film of the water and the substratum and thus to leave the water in the manner so well illustrated by Stichostemma. Perhaps Stichostemma itself will become able in time to resist evaporation and to obtain its food under

the altered conditions and so acquire a more or less completely terrestrial habit. At any rate this thigmotactic reaction to the surface tension of water must be regarded as one of the causes which may induce creeping aquatic forms to leave the water.

CHEMOTAXIS.

Among the chemotactic reactions the most conspicuous under conditions approaching the normal are the reactions to the composition of the water. In general the animals show some tendency to aggregate where the oxygen content is greatest. Placed in jars with masses of algæ and other animals, and kept where formation of oxygen by the plants does not occur in any marked degree, the animals aggregate at the surface as the water becomes foul. Under these conditions they are found either among the algæ just beneath the surface or crawling or resting beneath the surface film or about the margins. Furthermore, as the water becomes foul, animals which did not leave it earlier now crawl up the sides of the glass and die there. This reaction is in this case doubtless a mixed negative chemotactic and positive thigmotactic reaction; that is, the impulse to seek the surface is given by the increasing lack of oxygen or the increasing quantity of decomposition products in the water. Having reached the surface and being perhaps still restless in consequence of the chemical stimulus from the composition of the water, the worm leaves the water in response to the combined stimuli, and thus dies more quickly than it would if it remained in the water, since it possesses a high degree of resistance to the effects of foul water.

ENEMIES.

In general, Stichostemma appears not to suffer greatly from the attacks of predatory animals. Mutilated specimens are rarely found, though experiments show that even relatively small pieces of the body may live for weeks. Montgomery ('95) stated that cyprids destroy *Stichostemma eilhardi*. Under ordinary conditions I have never been able to observe that

cyprids actually attacked the active, healthy specimens. Occasionally they crawl over the body, but very soon leave it again, apparently without inflicting injury. In a series of experiments in which two or three specimens of Stichostemma were placed in small jars of clear water with hundreds of cyprids, it was found that although the worms remained alive and apparently uninjured for a day or two, they were finally completely devoured. When specimens of Stichostemma were cut in pieces and thrown into a jar containing numerous cyprids, they were rapidly devoured. In other experiments two or three worms were placed in a small dish with several dragonfly nymphs, which were given no other food. The nymphs occasionally attacked the worms, sometimes biting them in two. Within two days the worms were usually bitten into several pieces or killed, but not devoured. At the conclusion of the experiments the same nymphs took Gammarus eagerly, thus showing certainly that they were not satiated with food. Their attacks upon Stichostemma were often observed. The worms were picked up and held by the large labium for a moment, sometimes bitten completely through and allowed to drop almost immediately, or occasionally bitten at various points and badly crushed, but not eaten so far as could be observed. The worms frequently crawled over the surface of the nymphs without exciting any response from the latter. It is of course possible that the nymphs devour small portions, but they are certainly not sufficient to satisfy the hunger of these voracious feeders.

The worms are unable to escape from predatory forms by rapid movements, for their movements are all relatively slow. It was very evident during the experiments that the nymphs often saw the worms when at some little distance from them and approached them, perhaps reaching out and grasping them for a moment only to let them drop again. In such cases the nymphs had not the slightest difficulty in approaching the worms.

It would appear that Stichostemma, especially when filled with eggs, would afford an inviting morsel for many predatory aquatic forms, and that without some means of protection its

existence in the presence of such forms in the large numbers that occur would be impossible. Its conspicuous color and slow movements render it easy of discovery and approach by those forms which use the sense of sight in finding their prey. Nevertheless the adult, the young, and the eggs appear to remain unharmed in most cases.

I am inclined to believe that the abundant secretion of slime from the surface of the body and its increase under irritation renders Stichostemma more or less undesirable as an article of food. The slime is rather tenacious, and it is possible also that small animals are unable to pierce it and thus reach the body of the worm.

The bodies of the worms when cut into pieces possess a slight but distinct fishy odor. As was determined by direct experiment, no decided taste is present. It may be, however, that the slime or the body possesses some quality which renders it disagreeable to at least some animals; but even if this is not the case, the presence of the slime must afford a certain amount of protection against attacks, at least against those of small animals.

In connection with the possibility that the slime may afford a means of protection, it is interesting to note that in the experiments with the cyprids the nemerteans became very quickly surrounded by the slime covering and remained enclosed in it until they were artificially removed the next day. In all probability the rapid formation of the slime "cysts" was the result of the incessant irritation of the surface of the worm by the cyprids crawling over it. As it formed and thickened, this slime furnished a covering which the cyprids could not penetrate, or could penetrate only with difficulty after some time.

SEXUAL RELATIONS.

According to Montgomery, *Stichostemma eilhardi* is a protandric hermaphrodite. *Stichostemma asensoriatum* is hermaphroditic, but certainly not protandric. I have never found a purely male specimen of any size. The gonads are visible in the living animals, and the small oöcytes can be seen very early

in their history. Moreover, eggs and spermatozoa leave the gonads together when the eggs are laid. By subjecting the animal to pressure the spermatozoa may often be seen in the same gonads with fully grown oöcytes, and when the egg leaves the body there are nearly always a considerable number of spermatozoa sticking to its membrane. The contact with the water apparently serves as a stimulus, and fertilization as well as maturation occurs very soon after the egg leaves the body.

From these relations it is evident that self-fertilization is possible. As a matter of fact it is undoubtedly the rule. In a large number of cases specimens which had been isolated for a week or two laid eggs, and these were always fertilized and developed. I have often removed the eggs artificially by cutting the animal into pieces, and in every case where fully grown eggs were present, fertilization occurred. The fully grown eggs can be distinguished by the fact that no peduncle of attachment is present. In younger eggs the membrane is incomplete, and the egg is in continuity with the protoplasm of the gonad through a small stalk or peduncle. I have never been able to obtain unfertilized eggs. Finally, sections of the animal with full-grown egg cells always show the spermatozoa clustered over the surface of the egg or massed in some part of the gonad, while specimens with younger egg cells show stages of spermatogenesis, and still younger stages show merely the young oöcytes and the sperm mother-nuclei. The spermatozoa, or some of them, always pass out with the egg, and I believe that each egg is fertilized by the spermatozoa of the same gonad. There is absolutely no evidence that spermatozoa reach the oöcytes in any other manner. None have ever been found in the slime which encloses the egg after it is laid in the normal manner. None have been found in the water in which many specimens had been kept. But I think the strongest evidence in favor of self-fertilization lies in the fact noted above, that spermatozoa can be seen upon the membrane of each egg cell and that the penetration of these spermatozoa can be observed immediately after the egg cell reaches the water. As in *S. eilhardi*, the genital pores are not preformed,

so that spermatozoa cannot enter from the exterior before egg-laying unless they make their way through the body wall. That this is not the case is shown very clearly by the time of their appearance, their relations to the remainder of the gonad, and by the fact that fertilization itself always occurs outside of the body. The structure and relations of the various parts of the gonads and the oögenesis afford a large number of interesting facts, but these need not be discussed in detail here. There is strong evidence that each gonad is always hermaphroditic after its original formation, and that egg cells and spermatozoa almost always develop together.

I believe that cross-fertilization occurs very rarely in Stichostemma in nature, even if it ever occurs. The egg cells when they pass out of the body are immediately enclosed in the slime from the surface, and the spermatozoa with them. While it is, of course, possible that a few spermatozoa might make their way through the slime to the water and then again through the slime surrounding the eggs of other individuals, the most careful observations have never given the slightest evidence that this actually occurs. Furthermore, if it did occur, the second set of eggs would be fertilized before such a spermatozoön could reach them.

The only possible conclusion is that self-fertilization is the rule in *S. asensoriatum*.

As a rule only one egg is formed in each gonad, but exceptions are not uncommon, though more than two egg cells in a single gonad have never been observed.

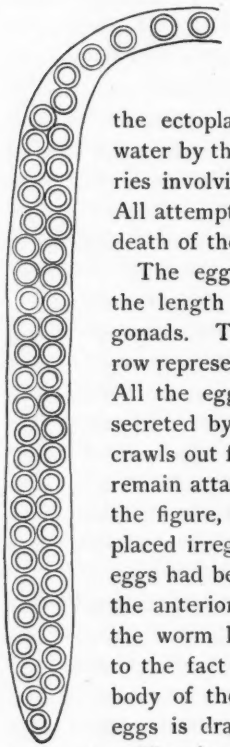
EGG-LAYING.

The normal process of egg-laying has not been observed in Stichostemma, although numerous egg strings have been found in the jars in which the animals were kept. The extrusion of eggs from the body in consequence of irritation or injury has often been observed. If an individual containing fully grown eggs be cut into several pieces, the eggs, or many of them, will often be extruded after a short time, apparently as the result of contractions following the injury. The first step in the

process is the breaking of the body wall at a definite point, *i.e.*, the appearance of the pore. Immediately after this the egg begins to flow out. The diameter of the pore is very small, so that the egg is greatly distorted during its passage. Indeed, it appears to flow out like rather thick fluid. At first a small, rounded, transparent protuberance appears at the outer opening of the pore; this is the egg membrane. Then the yolk granules and cytoplasm may be seen flowing out through the pore, and the part outside increases continually in size as more and more of the egg substance reaches it. The part of the egg outside the pore and that still within the body are connected by the slender band of egg substance which is passing through the body wall. The nucleus usually remains in the body until at least half of the volume of the egg has flowed out. The small size of the genital pore presents an obstacle to the passage of the nucleus, and often the passage of the egg ceases until some contraction of the body forces the nucleus through the narrow duct and it suddenly pops out through the pore. After the passage of the nucleus the remaining portion of the egg flows out rapidly, and the whole egg assumes almost immediately its spherical or nearly spherical form. The spermatozoa on the egg membrane can often be seen clearly during the passage of the egg, and it is evident that their movements begin as soon as they reach the water.

It is difficult to understand how definite areas of differentiated protoplasm could persist or maintain their proper position during this outflowing of the egg. To all appearances, at least, the egg flows out like a thick liquid under some pressure, and it appears scarcely possible that its parts maintain the same relative position before and after its emergence. The whole egg is enclosed, however, in a very thin layer of transparent protoplasm, an ectoplasm, and if the pressure is too great this layer is ruptured, and the cytoplasm and yolk flow out as a viscid, granular fluid, which tends to reassume the spherical form. It is evident that the cytoplasm is elastic and that the reassumption of the spherical form by the egg is due to this elasticity. Eggs in which the ectoplasmic layer has been ruptured do not develop, or at least development is confined to

the uninjured portion. All such cases of partial development die in early stages. When the yolk is exposed it appears to absorb water very rapidly, the egg or the injured part of it increases in size and becomes more transparent, and sections show vacuoles in place of the yolk granules. The death of the egg always accompanies or follows this absorption of water. Apparently the presence of the ectoplasmic layer prevents this absorption of water by the yolk. The egg is very sensitive to injuries involving the rupture of the ectoplasmic layer. All attempts to kill a part of the egg ended in the death of the whole a little later.



Egg string of Stichostemma.

The eggs are laid normally in strings of about the length of that portion of the body containing gonads. The eggs are deposited in two rows, each row representing the eggs from one side of the body. All the eggs are enclosed as they emerge in slime secreted by the dermal glands, and then the worm crawls out from between the two rows of eggs which remain attached to the substratum. As shown by the figure, the eggs at one end of the string are placed irregularly, as if the secretion enclosing the eggs had been stretched. This end is undoubtedly the anterior end of the string, *i.e.*, the end at which the worm leaves after laying, and its form is due to the fact that some of the slime adheres to the body of the worm, and together with the enclosed eggs is dragged after it as it moves away.

The cleavage of the eggs is typically spiral, all the cells being nearly equal in size during the earlier stages. The development is of the direct type. The surface of the embryo becomes ciliated, and it moves about within the egg membrane for a day or more before leaving it. The spherical embryo begins to elongate after three or four days, leaving the membrane when about one-half millimeter in length. The young animal possesses at first four eyes, the posterior pair of the adult being formed at a later stage than the others, thus

probably indicating their later origin in the species. I have not been able to ascertain whether the food of the young is the same as that of the adult.

The Breeding Season and its Relation to the Environment.

The breeding season of Stichostemma extends from May to November or December, according to the temperature of the water. Practically every specimen taken soon after the ice melts in the spring contains the growing oöcytes in the gonads, and these reach their full size, and egg-laying begins as soon as the shallow water along the shores becomes sufficiently warm. During the whole of the season from May to November the very young worms are abundant in sizes, varying from a millimeter up, and the eggs are often found in the algæ with the worms.

Egg-laying occurs freely in the laboratory. Often when the algæ containing worms are brought in and allowed to stand for twenty-four hours, a large number of egg strings will be found near the surface and on the sides of the jar. Apparently the eggs are always laid during the night or in darkness when the animals are moving about freely. Even in jars of clear water and without food the eggs are often deposited abundantly during the first few days of captivity, but individuals which do not lay eggs during that time are not likely to do so later, though, as experiment shows, they contain fully grown oöcytes.

Eggs can be obtained in the laboratory at any time during the year when the worms can be found in moderate numbers. During December many individuals with oöcytes at least half grown are found. In nature these eggs are probably not laid until the following spring, but if the worms are kept at room temperature in the laboratory a number will usually deposit eggs within a week or two, and this will occur even if the animals are kept without food. By these observations and those made upon animals under natural conditions during nearly two years, I am convinced that the limits of the breeding season are determined chiefly by the temperature of the

water. Probably food is actually an important factor, but its abundance is also more or less dependent on the temperature of the water, so that the latter must be regarded as the most important factor in determining the time of egg-laying.

That food is not of prime importance is clearly shown by a large number of observations in the laboratory. In animals which contained only small oöcytes when taken, and which are kept in clear water without food, the growth of the oöcytes will continue, and within a week or two eggs may be laid. This has been found to be the case even during the winter, and it shows very clearly that the important factor is the degree of temperature which permits the metabolism necessary for the formation of the yolk and the growth of the oöcyte in general. In such cases the oöcytes complete their growth either at the expense of the other tissues or some store of nutritive substance within the body. The body of the animal may even decrease somewhat in size during the growth of the oöcytes. In some way the energy of the body is applied to the completion of these important products, even at the expense of the remainder.

If an individual containing young oöcytes of small size be cut transversely near the middle of the body, and the pieces placed in clear water without food, both will usually live for months. The posterior piece does not regenerate, but the oöcytes grow much more rapidly in it than in the anterior half, and may attain their full growth and be capable of fertilization and development before those contained in the anterior half have reached more than half or two-thirds of their full size. I can explain this fact only on the basis of the difference in activity of the two halves. The anterior half, possessing a head and brain, behaves like a normal animal, moving about actively, while the posterior half, being without a brain and never regenerating a head or brain, is much less active and less sensitive to stimuli. In other words, much of the potential energy of the body which is employed in the anterior piece in producing the various movements, and probably in a more intense general metabolism, is directed in the posterior piece to the completion of the

growth of the oöcytes. These cases afford a most instructive example of the relation to each other of some of the various so-called vital activities. In the presence of the brain and anterior portion of the nerve cords the bodily movements appear to take precedence over other functions, even though the sexual products are not completed. But when the anterior portions of the nervous system are absent the animal, being without the power of regenerating the lost parts, is less affected by stimuli, and a larger portion of the potential energy is devoted to the elaboration of the sexual products. This process must, as a matter of fact, be regarded as the function next in importance to that of carrying out the normal movements and responses to stimuli.

Mention has been made of the fact that animals kept in captivity without food are not likely to deposit their eggs after the first week or two of captivity, even though artificial removal of the egg cells may show them to be capable of fertilization and development. In such cases the fate of the egg cells is quite remarkable. They may remain unchanged in appearance for two or three weeks, but after a time evidences of alteration in their structure are visible even in the living animal. The egg cells become less opaque in appearance and a clear space appears about each, apparently the result of thickening and swelling of the membrane. Later many of the eggs break up into round masses and granules, which sections show to be merely disintegration products and not cells. But the more remarkable fact is that, as the changes go on, many or all of the eggs pass out of the gonads and come to lie within the alimentary canal, where they serve as food and are actually digested. Continued observation from day to day of isolated specimens leaves no doubt that this actually occurs. In many cases the egg cells are still intact when they enter the alimentary canal and can clearly be seen there, moving to and fro with the movements and contractions of the body. Disintegration and digestion of the egg goes on rapidly in the alimentary canal, however, and in a day or two the whole intestine may be filled with a granular mass which represents the cytoplasm and yolk of the egg. In case disintegration of the egg has begun before it enters

the alimentary canal, it very rapidly becomes a granular mass recognizable as an egg only through its known origin.

That these disintegrating eggs actually serve the animal as food is evident from the fact that in a number of cases the passage of the eggs to the alimentary canal and their digestion was followed in a few days by the appearance and partial growth of new oöcytes in the gonads, each individual worm being isolated meanwhile in clear water and without other food during the whole period. In cases where the eggs were normally laid by similarly isolated specimens, new oöcytes appeared only when the first set had been laid almost immediately after the beginning of the experiment, so that the animal was comparatively fresh and probably still contained a certain surplus of nutritive material. Moreover, these oöcytes never reached a large size and usually underwent disintegration at a later period.

The manner in which the disintegrating egg cells reach the alimentary canal is somewhat obscure. Rupture of the walls of the gonad and the intestine is necessary. I believe that this rupture is brought about chiefly in consequence of the increasing disproportion between the size of the body and the size of the egg as the starving animal decreases in size, and that finally the egg becomes too large for the lateral regions of the body and is forced into the alimentary canal by the movements and contractions of the body. A study of sections reveals a decreasing thickness in the walls of the intestine and gonads, as well as other histological changes, but these need not be discussed here.

The passage of the egg cells to the intestine occurs in pieces which have been deprived of head and brain, as well as in normal individuals.

ABSENCE OF FISSION.

Benham ('97) has described a process of spontaneous fission in Carinella which probably serves as a means of distribution of the sexual products, and Wilson ('00) states that Cerebratulus fragments spontaneously at the close of the breeding

season, apparently as a means of getting rid of a portion of the body which has become of little use.

I have never observed spontaneous fission or fragmentation in Stichostemma, and have never found pieces or fragments which might be the result of such fission. Occasionally specimens are found which show slight constriction at some points, but isolation and continued observation of these individuals have always been without result. These constrictions appear not only in individuals with mature sexual products, but in other stages, and usually disappear after a few days. Moreover, they are frequently irregular, being more pronounced on one side of the body than on the other. I am inclined to believe that they are merely the results of slight injuries, for slight cuts in the sides of the body produce results which are indistinguishable from those found in freshly collected specimens.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO, July, 1901.

LITERATURE.

'97 BENHAM, W. B. Fission in Nemertines. *Quart. Journ. Micr. Sci.* Vol. xxxix.

'98 BÖHMIG, L. Beiträge zur Anatomie und Histologie der Nemertinen. *Zeitschr. f. wiss. Zool.* Bd. lxiv, Heft 3.

'01 HOLT, E. B., and LEE, F. S. The Theory of Phototactic Response. *Am. Journ. Physiol.* Vol. iv, No. 9.

'90 LOEB, J. Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen. Würzburg.

'93 LOEB, J. Ueber künstliche Umwandlung positiv heliotropischer Thiere in negativ heliotropische und umgekehrt. *Arch. f. d. ges. Physiol.* Bd. liv.

'95 MONTGOMERY, T. H. Stichostemma eilhardi *nov. gen., nov. sp. Zeitschr. f. wiss. Zool.* Bd. lix.

'96 MONTGOMERY, T. H. Stichostemma asensoriatum *nov. sp.*, a Fresh-Water Nemertean from Pennsylvania. *Zool. Anz.* Bd. xix, No. 515.

'97 MONTGOMERY, T. H. On the Connective Tissue and Body Cavities of the Nemerteans, with Notes on Classification. *Zool. Jahrb.*, Abth. f. Anat. und Ont. Bd. x.

'00 PARKER, G. H., and BURNETT, F. L. The Reactions of Planarians with and without Eyes to Light. *Am. Journ. Physiol.* Vol. iv, No. 8.

'85 SILLIMAN, W. A. Beobachtungen über die Süsswasserturbellarien Nordamerikas. *Zeitschr. f. wiss. Zool.* Bd. xli.

'97 VERWORN, M. Allgemeine Physiologie. Jena.

'00 WILSON, C. B. The Habits and Early Development of Cerebratulus Lacteus (Verrill): A Contribution to Physiological Morphology. *Quart. Journ. Micr. Sci.* Vol. xliii, pt. 1.

AN EXTRAORDINARY ANT-GUEST.[1]

WILLIAM MORTON WHEELER.

SINCE Sir John Lubbock's discovery of the association of certain Phoridæ (*Phora formicarum* Ver. and *Platyphora Lubbocki* Ver.) with ants,[2] several interesting additions to the number of known myrmecophiles and termitophiles belonging to this family of Diptera have been recorded. Among others a singular group of wingless Phoridæ ("Stethopathidæ") has been described by Wasmann[3] from specimens captured in the nests of termites, and Brues has recorded the occurrence of several somewhat similar forms in the nests of certain Texan ants belonging to the genera Eciton and Solenopsis.[4] Very recently Pergande[5] has published an entertaining note on the habits of a phorid (*Apocephalus pergandei* Coq.) which causes the workers of the common wood-ant (*Camponotus pennsylvanicus*) both figuratively and literally to "lose their heads," for the interior of this important portion of the ant's body furnishes the fly-larva with food and a retreat for pupation.

Far less injurious to its hosts is a myrmecophilous phorid which I propose to describe in the following pages. Unfortunately I have seen only its larval and pupal stages, but these are passed under such unusual circumstances that the discovery of the imaginal insect could scarcely supply details of very great additional interest. As the insect is not very common, many months may pass before I am able to complete my study

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, No. 23.

[2] Lubbock, Sir John. *Ants, Bees, and Wasps.* 1881.

[3] Wasmann, E. Termitoxenia, ein neues flügelloses, physogastres Dipterengenus aus Termitennestern, *Zeitschr. f. wiss. Zool.*, Bd. xlvii, No. 4 (1900), pp. 599–617, Taf. XXXIII.

[4] Brues, C. T. Two New Myrmecophilous Genera of Aberrant Phoridæ from Texas, *Am. Nat.*, vol. xxxv, No. 413 (May, 1901), pp. 337–356, 11 figs.

[5] Pergande, Theo. The Ant-decapitating Fly, *Proceedings Ent. Soc. Wash.*, vol. iv, No. 4 (1901), pp. 497–502, 2 figs.

of its life history. There is some excuse, therefore, for publishing these fragmentary observations.

On October 27 of last year I made a short excursion to Mt. Barker, which is hardly more than an hour's walk from the university at Austin, Texas. The woods about the base and on the slopes of the elevation are favorite nesting grounds for the large black ponerine ant, *Pachycondyla harpax*. In October this ant is rearing its second brood of larvæ and pupæ, having completed the education of its first brood during June and July.[1] Wishing to continue some observations on the habits of Pachycondyla, I dug up one of the largest nests I could find and carried it home in a bag. On transferring it to a Lubbock nest I took the census of the colony and found it to comprise 25 worker ants, 13 cocoons, 8 mature larvæ, 7 immature larvæ, and a packet of eggs. While counting the larvæ, which are shaped like the well-known cucurbitaceous product known as the "crook-necked squash," and covered with hairy tubercles, I noticed that six of the largest and one of the smallest presented an unusual appearance. Each of these seemed to wear about its neck a huge collar, — a sort of Elizabethan ruff, — consisting of a curled larva. That this could not be another ant-larva was apparent from a moment's examination. In all cases it almost completely encircled the ant-larva in the region of the first abdominal, or in some cases the metathoracic, segment. The posterior end was provided with a sort of disk, which adhered so tightly that both larvæ could be killed in alcohol without separating. The collar-like larva was broad behind the middle, but tapered anteriorly to a very slender thoracic region and head provided with small jaws. These were supported by a chitinous frame-work of such characteristic structure as to show that the adult form must be a true dipteron fly. The very smooth and tense integument, which was armed with some short, hooked bristles, was very transparent, so that the peristaltic movements of the viscera were clearly visible. One of the adult Pachycondyla larvæ with its living collar is shown in Fig. 1.

[1] For an account of the habits of this ant, see my paper, A Study of Some Texan Ponerinæ, *Biol. Bull.*, vol. ii, No. 1 (Oct., 1900), pp. 1–31, Figs. 1–10.

As soon as the ants had been transferred to the Lubbock nest they were given a number of young larvæ of *Camponotus sansabeanus*. These they soon proceeded to malaxate with their mandibles, twirling the morsels about in the mean time with their fore legs and lapping up the exuding juices with their tongues. Finally they deposited the crumpled and pulpy remains of the Camponoti on the trough-like ventral surfaces of their larvæ, which had been previously placed on their backs in a rough chamber dug in the earth of the nest. This chamber was immediately under the glass roof-pane, so that further developments could be closely observed with a pocket lens. Each ant-larva at once stretched forth its head eagerly and began to devour the viands with which it had just been provided. At the same moment the dipteron larva, too, as if sniffing the odor of the fresh food, unwound its tapering neck from the ventral surface of its host, and, without shifting the attachment of its posterior end, at once plunged its mandibles into the food. Under the lens both larvæ could be seen greedily dining side by side till the last particle of the Camponotus larva had been consumed or prematurely removed by the worker ants.

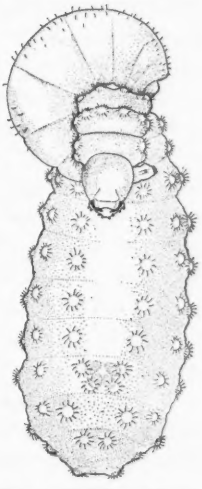


FIG. 1. — Adult larva of *Pachycondyla harpax* bearing a commensal phorid larva.

When the ant-larvæ were huddled close together, a collar-like larva was sometimes observed to reach over and help itself from the food supply of a neighbor; but even when thus compelled to crane its neck to the utmost, it never shifted the attachment of its caudal end. Sometimes when there was no food within reach it would tweak with its sharp little jaws the sensitive hide of a neighboring ant-larva, till the latter squirmed with pain. It would sometimes even tweak its own host, as if to make it wriggle and perhaps thereby incite the worker ants to bring a fresh supply of provisions.

The following day two living myriopods (Lithobius) were

placed in the nest. During the morning hours they were killed by the Pachycondyla workers, shorn of their many legs, cut up into pieces of convenient length, malaxated, and fed to the larvæ as on the preceding day. And again I was able to witness the strange banquet — the dwarf reaching down from the shoulders of the ogre and helping himself from the charger formed by the trough-like belly of his host. The same observation was repeated on several successive days. Pieces of various ant-larvæ, beetle-larvæ, Lithobius, Scutigera, Oniscus, — all were served up to the ant-larvæ and partaken of with great relish by the dipteron larvæ as well. There could be no doubt that the latter were true commensals, — perhaps the most perfect commensals, in the original meaning of the term, to be found in the whole animal kingdom!

As one of the smallest Pachycondyla larvæ, scarcely one-fourth grown, bore a very small dipteron larva, it is, perhaps, safe to say that the ant-larva acquires its commensal at a very early age. The two then grow up together, so that there is always a certain relation between the two kinds of larvæ — large Pachycondyla larvæ bearing large commensals, and *vice versa*. The worker ants lick and cleanse the commensals at the same time that they are caring for their own larvæ. This is usually done just after meals. Since, during this operation of cleansing, the ants spend no more time over the commensals than they do on a similar area of the body surface of their own larvæ, it would seem that they are not even aware of the existence of the commensals. To these nearly blind ants, which must rely almost exclusively on their senses of touch and smell, the larvæ bearing commensals, if distinguished at all from individuals without such attendants, would probably be perceived merely as having unusually protruding necks. But there is nothing to indicate that these insects are really capable of perceiving such differences in their environment.

At this time an amusing interlude in these observations was furnished by introducing into the nest a few living "pill-bugs" (Armadillidium sp.). For two whole days the Pachycondyla workers hunted these isopods from one corner of the nest to another. An Armadillidium would scurry along rather quickly

and, when overtaken, escape death by rolling itself up into a hard ball, which the ants tried in vain to perforate with their mandibles. As soon as they desisted the Armadillidium would unroll itself, and the chase would begin again. Finally I was compelled to remove the crustaceans, as the larvæ seemed to be in danger of being injured in the excitement of the chase.

On the 5th of November I obtained satisfactory evidence that the dipteron larva is not obliged to remain always with the same Pachycondyla larva. During the night one of the large larvæ had moved and attached itself to the first abdominal segment of an ant larva which already bore a commensal around its metathoracic segment. The two larvæ were oriented in opposite directions, *i.e.*, with their heads reaching around opposite sides of their host. Subsequently one of these commensals moved to an unoccupied Pachycondyla larva. I was not present when the change occurred, nor was I able to determine whether it was the originally stationary or the adventitious larva that moved. Although this observation makes it certain that the dipteron larvæ can shift their position from one host to another, I am convinced, nevertheless, that they must do this with great reluctance and only under urgent circumstances, such as extreme hunger, the death of the larva to which they are attached, or, perhaps, when fully mature and about to pupate.

As the days passed, the mature ant-larvæ spun their brown cocoons one by one, and one by one the mature commensals disappeared. Did they also pupate and for this purpose conceal themselves in the soil of the nest? or had the ants at last detected the villains and converted them into food for the larvæ which had not yet pupated? or did they stick to their hosts and pupate within the cocoons? In order to ascertain, if possible, the true state of affairs, I transferred the whole colony to a fresh nest and examined the soil of the old nest with great care. There were no traces of the missing commensals. The only remaining resource was to open the cocoons. Several of the cocoons which had been taken with the nest October 27 had hatched, but by November 10 there were still thirteen cocoons in the nest, as several of the larvæ had pupated in the mean time. Five of these were opened, and in two,

which contained pseudonymphs of Pachycondyla and were, therefore, of recent formation, commensals were found! Having shared the table of their host, they had come to share its bed as well. The dipteron, too, had pupated after the manner of its kind — forming a puparium; *i.e.*, instead of spinning a cocoon like the ant-larva, the dead larval skin, somewhat shriveled and contracted, was used as an envelope, and within this the pupa proper was formed.

This puparium, represented in Fig. 2, is from 2.25 to 2.5 mm. long and clearly of the cyclorhaph type. It is elliptical, much flattened dorso-ventrally, especially along the edges, which are thin and hyaline and almost alate. The brownish dorsal surface is thrown into delicate and irregular transverse wrinkles. Anteriorly, in the thoracic region, there is a pair of short black respiratory tubes. The ventral surface is very glabrous and distinctly paler than the dorsal surface. From its small size, cyclorhaphous character, and resemblance to the puparium of a typical Phora bred by one of my assistants, Mr. C. T. Brues, from some spider's eggs, I conclude that the insect under consideration must be one of the Phoridæ.

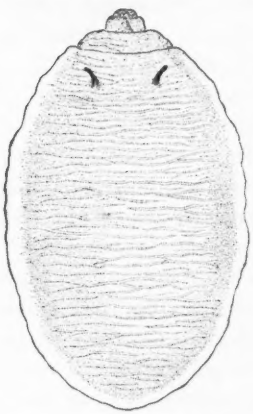


FIG. 2. — Puparium of phorid commensal from the cocoon of *Pachycondyla harpax*.

Subsequently, several other cocoons were opened and two more were found to contain the puparia of commensals. In all four cases the puparium was invariably located in the caudal pole of the cocoon, just to one side of the black blotch of ejecta deposited by the ant-larva before becoming a pseudonymph. At this point the puparium was immovably stuck to the wall of the cocoon by means of its smooth ventral surface. Its anterior end was directed towards the cephalic pole. As there is always considerable space, especially at the posterior pole, between the walls of the cocoon and the enclosed ant-pupa, the much-flattened fly puparium did not in the least crowd its host.

Reflection shows that the position of the puparium in the posterior pole of the cocoon, though the reverse of the position of the larval commensal with respect to its larval host, is the only one which can be maintained by the commensal with perfect safety. Like other ants, the Pachycondyla leaves its cocoon through a rent in the anterior pole. This rent is certainly made by the mandibles of the hatching ant, and it is possible that the callow insect may succeed in making its way out of the cocoon without any assistance from the workers. I have hitherto failed, however, to surprise one of these ants in the act of hatching. But even if the obstetrical aid of the workers is necessary, as it is in the more highly specialized Camponotinæ, any position for the commensal puparium, except at the posterior pole of the cocoon, might be fatal, for the struggling jaws and legs of the emerging ant and the jaws of the assisting ants would certainly be very liable to cut into any delicate object attached to the anterior or median walls of the cocoon. This danger, of course, would not exist if the fly hatches before the ant and is able to perforate the cocoon and escape. It is altogether more probable, however, that the ant hatches before the fly in the manner suggested below.

It would be interesting to know what the commensal larva is doing while the ant-larva is weaving its cocoon. Does it move about to avoid the swaying jaws of the spinning larva? or does it take up its position from the first at the posterior end of the larval ant and there remain motionless while the posterior pole of the cocoon is being completed? It is very difficult to answer these questions. The fact that the posterior poles of all the cocoons containing puparia were somewhat distorted, being broader, more obtuse, and more irregular than the normal cocoons, would seem to indicate that the ant-larva may modify this end of its cocoon for the better accommodation of the commensal. I am inclined to believe, however, that the distortion may be produced by the dipteron larva while attaching itself just before pupating to the newly woven and still plastic cocoon.

At this point my observations end. The phorid puparia were kept for several weeks in what I supposed to be the proper conditions of warmth and moisture, but to my intense

disappointment they failed to hatch. During the autumn and winter frequent and diligent search was made for more of the commensals in all the Pachycondyla nests I could find, but in vain. Finally, during the latter part of May of the current year, I discovered in a very different locality two Pachycondyla nests which contained a few phorid larvæ. This discovery proved that the phorid is double-brooded like its host. But the larvæ were very small and attached to such very young ant-larvæ that I despaired of being able to raise them in my artificial nests as far as the imaginal stage. It remains, therefore, for the future to fill this gap in my observations.

As a small contribution towards filling this gap I venture to advance the following conjecture concerning the circumstances under which the phorid fly probably hatches. I assume that the ant must hatch before the fly. Now very soon after the former hatches the useless cocoon is always carried by a worker and placed on the refuse heap, which in the natural nest is often almost entirely made up of the empty cocoons of from one to several broods of ants, and lies in a rather dry and well-ventilated spot immediately beneath the stone covering the nest. Along with the cocoon is carried the phorid puparium still adhering to the wall at its unopened posterior end. Thus after a privileged existence as free pensioner and bedfellow to a generous host, it is unwittingly carried away in the worn-out bedclothes and consigned to the family rag pile. Here the small and probably very active fly hatches, leaves by the wide-open front door of the cocoon, and, after mating, either returns to lay a few eggs in the galleries of its former host, or flies away to oviposit in some other Pachycondyla nest. Thus the simple assumption that the fly hatches later than the ant renders it unnecessary to suppose that the fly possesses some peculiar means of perforating the tough wall of the cocoon, and also accounts for the position of the puparium in the posterior pole, where it would be completely concealed from the workers even after the escape of the callow ant.

In conclusion the reader's attention may be directed to certain particulars of special interest in connection with the life history of the Pachycondyla commensal:

First, the peculiar habits of the phorid show clearly that the ponerine method of feeding the larvæ with comminuted insects is not only the typical but the only method employed by these ants, for such a commensal would certainly starve if the Pachycondyla larvæ were carefully fed like the larvæ of Camponotus and Formica, by regurgitation of liquid food from the mouths of the workers. The phorid profits by a peculiarity in the behavior of its host, and thereby demonstrates — by one of Nature's experiments — that *Pachycondyla harpax* cannot feed its young by regurgitation.

Second, in the peculiar symbiotic relationship existing between the phorid and the ants, the adaptations are all on the part of the former, whereas the latter pursues its ancient and well-established mode of life uninfluenced by and apparently in complete ignorance of the very existence of its little guests. Even the distortion of the cocoon may be due, as I have suggested, entirely to the activity of the phorid. These strikingly unilateral adaptations are probably to be explained on the ground that the phorid in the Pachycondyla nest is as careful and conservative — if such terms may be used — of the life and welfare of its host as Pergande's Apocephalus is ruthless and destructive. The small amount of food consumed by the former can hardly be a serious drain on the provisioning instincts of the Ponerinæ. The larvæ bearing the commensals were certainly as large and healthy as any others in the nest, and produced perfectly normal pupæ, which in the cases observed all lacked the imaginal disks for the wings and were therefore of the worker type. Whether the presence of the commensals by reducing the amount of food even to a slight degree could inhibit the development of queen larvæ and thereby convert them into workers, involves a problem as interesting as it is difficult to solve in the present state of our knowledge.

Third, the commensal of Pachycondyla, together with the Phoridæ mentioned in the introductory paragraph of this paper, shows that the flies of this family are well worth careful study. While the Stratiomyidæ, Syrphidæ, Midaidæ, etc., certainly make more attractive cabinet specimens and prettier monographic plates, it is very doubtful whether the life

histories of most of these conspicuous Diptera can compare in interest with those of the tiny, dull-colored Phoridæ. That the study of the smaller and inconspicuous Diptera, like the Culicidæ, has been unduly neglected is clearly shown by recent medical researches on the malaria parasite.

COLEBROOK, CONN., August 16, 1901.

FRIEDENTHAL'S EXPERIMENTAL PROOF OF BLOOD-RELATIONSHIP.[1]

HERBERT W. RAND.

In recent years important evidence in favor of Darwin's theory of the descent of man has increased. Eugen Dubois found in *Pithecanthropus erectus* the much-sought-for missing link between man and living anthropoid apes. Selenka has shown that, of the catarrhine apes, the living anthropoid apes resemble man in having a placenta discoidalis capsularis, while all other catarrhines have a placenta bidiscoidalis. Ernst Haeckel has accumulated evidence showing that man has descended from a line of extinct catarrhines whose immediate ancestors belonged to the group of tailless anthropoid apes, and whose more remote ancestors belonged to the Cynopithecini. The evidence afforded by comparative paleontology, comparative embryology, and comparative anatomy agrees in supporting Darwin's hypothesis.

To all this evidence is now added evidence depending upon the similarity in chemical composition of the blood of closely related animals. Comparative chemical analyses of blood are attended with great difficulties because of variations in the blood depending upon the varying conditions of nutrition in the animal. Landois, in his researches on the effects of animal blood transfusions upon human diseases, attributed his failures, so far as the beneficial effects of the blood transfusion upon the disease were concerned, to the dissolving of the red blood corpuscles of the injected blood by the blood of the recipient. Experiments upon lower animals, in the way of injecting blood from some animal of a remote species, led to the same results as the experiments upon man. The animals

[1] An extended abstract of a paper by Hans Friedenthal: Ueber einen experimentellen Nachweis von Blutverwandschaft, *Archiv für Anatomie und Physiologie*, physiologische Abtheilung, Hefte 5 und 6, 1900.

exhibited pathological conditions with development of fever, or very often died soon after the transfusion. The hemoglobin of the foreign erythrocytes appeared in the bladder immediately after the transfusion, and often more hemoglobin was given off than was contained in the injected blood. The dissolving of red blood corpuscles by the serum of foreign blood was first observed under the microscope by Creite.

Landois found, in some cases, that the dissolving of the injected blood elements did not occur. In transfusions between the horse and ass, wolf and dog, rabbit and hare, no hemoglobin appeared in the urine; the animal, even after the injection of a large amount of blood, showed no pathological symptoms, but behaved precisely as after an injection of blood from one of its own kind. Landois concluded that *only animals of very closely related species can exchange blood with impunity*. The question then arises, How closely related must animals be in order that their blood may be "physiologically identical"?

The method of blood transfusions is not adapted to extensive comparative researches. But the "globulicidal" action of a blood serum can be observed to advantage in a test-tube. To 10 c.cm. of the serum of some mammal let there be added three drops of foreign blood from which the fibrin has been removed, and let the mixture be kept at 38° for fifteen minutes. The mixture is at first opaque, because of the added erythrocytes, but at the end of the fifteen minutes the fluid regains its transparency and acquires a bright red, owing to the dissolving of the coloring matter from the added red corpuscles. Buchner found that if the serum is heated to 55° its power of dissolving foreign corpuscles is quite lost. Buchner also found that serum would dissolve the white corpuscles of foreign blood.

The loss of the dissolving power of serum as a result of raising the temperature shows that the dissolving power depends upon chemical and not upon physical factors, since, by heating, the osmotic tension of the serum is not changed.

The blood of cold-blooded animals does not respond to the test so readily as the blood of mammals, the nucleated corpuscles evidently possessing greater resistance. Non-defibrinated mammalian blood requires longer for the dissolving of its

corpuscles than if the fibrin be removed. Control experiments with superheated serum show that the dissolving, which does at length occur, is not due to the action of bacteria developed in the serum. On the contrary, the dissolving power of the serum is inhibited by the increase of bacteria.

Thus far the dissolving action of serum has been demonstrated only among vertebrates. So far as tried, the blood of invertebrates (Cancer, Arenicola, sea-urchin) has no globulicidal effect upon the erythrocytes of vertebrates (gull, rat). Among cold-blooded vertebrates the action is so slow as to be best observed under the microscope. Only the serum of Anguilla acted so rapidly as to make macroscopic observation easy. It was noted that sera which are particularly poisonous, such as the serum of Anguilla, the domestic fowl, and cat, act most rapidly upon corpuscles. This suggests that both effects are due to chemical substances of the same class.

The serum of Anguilla dissolves the corpuscles of mammals, birds, reptiles, and amphibians, and also that of other fishes. The blood of *Acanthias vulgaris* is quickly dissolved by Anguilla serum, and so is the blood of other teleosts, as *Labrus maculatus*. The effect of Anguilla serum upon the blood of other Murænidæ was not tried. The serum of Acanthias dissolves the erythrocytes of the gull, mouse, and of teleosts (Labrus, Anguilla). It is not entirely indifferent toward the blood of other elasmobranchs (*Raja batis*).

Among Amphibia, Anura are easily distinguished from Urodela by difference in blood. Frog corpuscles are dissolved by the serum of Anguilla, the gull, and cat. The dissolving power of amphibian blood is less in animals that have been kept in captivity for some time and poorly fed.

Among reptiles, the serum of some snakes was found to exceed that of amphibians in globulicidal action. Yet more powerful is the action of bird serum. This fact is parallel to the fact that the serum of birds is especially poisonous to other vertebrates. This common quality of the serum of reptiles and birds is correlated with similarities in anatomical structure which have caused reptiles and birds to be classed together as Sauropsida. The serum of the domestic fowl

dissolves the erythrocytes of animals from all other classes of vertebrates, and also of other birds.

The results of the experiments with sera of mammals agree entirely with the results of Landois's experiments with transfusions, but they do not agree with the results obtained by Ehrlich and Morgenroth, Bordet, and Gürber. This lack of agreement is doubtless due to difference in methods. The investigators named above washed out by isotonic salt solution all the serum from the erythrocytes of one animal and added large quantities of the erythrocytes to the serum of another animal. By this method in many cases no globulicidal action can be observed, while, if a small quantity of simply defibrinated blood be added to the serum, the erythrocytes are quickly dissolved. The importance of adding only small quantities of blood to the serum lies in the fact, observed by Buchner, that in the mingling of two different sera the globulicidal action may be either increased or diminished. In transfusion experiments the more blood injected the better.

The carotid arteries of a cat and an ocelot were connected so that an exchange of blood took place from one animal to the other. After a short time the blood of each animal was supposably well mingled with that of the other. No hemoglobin appeared in the bladder of either animal. The blood of the cat and of the ocelot is physiologically equivalent. If a cat and a rabbit be connected in the same way, both animals die in a few minutes from the poisonous effects of the foreign blood upon the central nervous system. Death occurs before any globulicidal action takes place. Two rabbits connected in this way exhibit no pathological symptoms.

The experiments upon mammals lead to the conclusion that among animals of the same family there are no marked differences in blood ; but the blood of animals of different suborders is not physiologically equivalent, while the blood of animals of different orders exhibits very marked mutual globulicidal action. The blood of the mouse and blood of the rat are mutually inactive. The blood of the hare and of the rabbit is equivalent; but rabbit serum dissolves corpuscles of the guinea-pig, and rabbit corpuscles are dissolved by serum of the guinea-pig,

these animals belonging to different families. The blood of the rabbit is equivalent only to that of the hare, of all the animals experimented upon.

Of Perissodactyls, serum of either the horse or ass is inactive toward corpuscles of the other, but horse serum dissolves corpuscles of the rabbit, guinea-pig, calf, lamb, and man.

Of Artiodactyls, the serum of either the ox or swine dissolves corpuscles of the other, and both dissolve corpuscles of the dog, cat, horse, rabbit, and man.

Of Carnivora, the blood of the dog, fox, and wolf is equivalent, but serum of either the dog or cat dissolves corpuscles of the other. The serum of either the cat, ocelot, or jaguar is inactive toward corpuscles of the other two animals, but cat serum dissolved the corpuscles of all the other mammals tried.

Finally, among primates, human serum dissolves the corpuscles of fishes, frog, snakes, pigeon, fowl, night-heron, horse, swine, ox, rabbit, guinea-pig, dog, cat, hedgehog, and lemur. The effect of human serum was tried upon the blood of six species of apes (the platyrhines, *Pithesciurus sciureus*, *Ateles ater;* the catarrhines, *Cynocephalus babuin*, *Macacus sinicus*, *Macacus cynomolgus*, and *Rhesus nemestrinus*, at the Berlin Zoölogical Garden). In all cases the human serum dissolved the ape corpuscles. The serum of Macacus had no effect upon the blood of some persons, while the blood of others was quickly dissolved by it.

Among the true anthropoid apes is first found blood which is physiologically equivalent to that of man. To 5 c.cm. of transparent human serum was added a drop of blood from the finger-tip of an orang-outang, and in another case from a gibbon, both young animals from the Berlin Zoölogical Garden. After twelve hours the red corpuscles were separated from the serum by the centrifuge, apparently having suffered no change, while the serum remained free from color. In three experiments, where 10 to 20 c.cm. of fresh, defibrinated human blood was injected into the veins of *Macacus cynomolgus* or *Macacus sinicus*, only a small quantity of hemoglobin appeared in the urine, — scarcely more than is found in the serum as a

result of the defibrinating process. The animals suffered no ill effects from the operation. Twenty-five cubic centimeters of human blood was injected into a ten-year-old chimpanzee. For two days the urine was tested and showed no signs of hemoglobin or albumen. The injected blood apparently produced no effects whatever. It has been shown by successful blood transfusion experiments that the blood of such widely separated races as the negro and white is physiologically equivalent.

These blood comparisons, as well as the embryological researches of Selenka, justify placing man and the anthropoid apes together in the same family, or at least in the same suborder, rather than isolating man in a suborder of primates, coördinate with the suborders of the platyrhines and catarrhines.

The chemical similarity of the blood of morphologically similar animals is not surprising. The thing inherited through the ovum and spermatozoön is not "innere Impulse," "Iden," or "Entwickelungsmöglichkeiten," but a certain definite chemical composition of the molecule. Development, form, and the nature of the metabolic processes are as closely dependent upon the chemical composition of the molecule as any chemical reaction is dependent upon the chemical composition of the reagent causing it. Similarity in the chemical composition of blood is but one factor in the chemical similarity of closely related organisms. The chemical similarity of reproductive cells must be regarded as an epitome of all the chemical similarities of the adults.

It is well known that the horse and ass, dog and wolf, rabbit and hare readily cross. It would be a valuable experiment to attempt, by means of artificial fertilization, a cross between the rat and mouse, or between the domestic cat and the ocelot. The physiological similarity of the blood of either pair of animals points toward the possibility of a successful crossing.

QUARTERLY RECORD OF GIFTS, APPOINTMENTS, RESIGNATIONS, AND DEATHS.

EDUCATIONAL GIFTS.

Alameda, California, $35,000, from Andrew Carnegie, for a public library.

Amherst College, $2000, by the will of Professor Herbert B. Adams.

Armour Institute, $250,000, from Mrs. Philip D. Armour and J. Armour.

Arnold Arboretum of Harvard University, $126,485, from various sources, for its endowment fund.

Barnard College, $1500, for fitting up the zoölogical laboratory.

Berea (Kentucky) College, $50,000, by the will of Stephen Ballard of Brooklyn.

Bethany (Kansas) College, a conditional gift of $25,000, from Dr. D. K. Pearson.

Burlington, Vermont, $50,000, conditional from Andrew Carnegie, for a public library.

Carson-Newman College, $45,000, from John D. Rockefeller; $15,000, from other sources.

Chatham, N.Y., $15,000, from Andrew Carnegie, for a public library.

Colorado College, $100,000, from an anonymous donor.

Columbia University, $100,000, from an anonymous donor, for a department of Chinese; $10,000, for the purchase of books; $5000, for a historical reading room; $5000, for general purposes, from an anonymous donor.

Cornell University, a conditional gift of $250,000, from John D. Rockefeller; an astronomical observatory and equipment, from General A. C. Barnes.

Dartmouth College, $100,000, from Amos Tuck, for a building for the school of administration and finance.

Des Moines (Iowa) College, a conditional gift of $25,000, from John D. Rockefeller.

Detroit, Michigan, $750,000, from Andrew Carnegie, for a public library.

Drury College (Missouri), $25,000, from Dr. D. K. Pearson; $25,000, from other donors, for a science building.

Eureka (Illinois) College, $60,000 in land, from Mrs. D. Bandy.

Fairmount (Kansas) College, a conditional gift of $25,000, from Dr. D. K. Pearson.

Fargo College, a conditional gift of $50,000, from Dr. D. K. Pearson.

Georgia State Normal School, a conditional gift of $13,000, from G. F. Peabody.

Hamline University, $50,000, from James J. Hill; $30,000, from M. G. Norton.

Harvard University, $1,000,000, from J. Pierpont Morgan, for buildings for the medical school.

Illinois College, a conditional gift of $50,000, from Dr. D. K. Pearson.

Kenyon (Ohio) College, $50,000, from Senator Mark Hanna.

Leadville, Colorado, $100,000, from Andrew Carnegie, for a public library.

Massachusetts Institute of Technology, $100,000, from the alumni, for a gymnasium; $10,000, from George A. Gardner.

McKendree (Illinois) College, a conditional gift of $50,000, from Dr. D. K. Pearson.

Middlebury (Vermont) College, $12,500, from Ezra J. Warner; $5000 from Dr. M. Allen Starr.

Milliken University (formed by the union of Lincoln College and the Decatur Industrial College), $150,000, from James Milliken.

New York Botanical Gardens, $3200, from Misses O. E. P. and C. P. Stokes.

Princeton University, $50,000, for a library fund; $10,000, for a fellowship; $150,000, from the alumni, for a gymnasium; $10,000 for a fellowship in biology, from Mrs. Maule.

Radcliffe College, about $200,000, by the will of Susan Cabot Richardson; $25,000, by the will of John Sweetser.

Riverside, California, $20,000, from Andrew Carnegie, for a public library.

Rockefeller Institute for Medical Research, $200,000, from John D. Rockefeller.

San Francisco, California, $750,000, from Andrew Carnegie, for library purposes.

Smith College, $28,000, by the will of Mrs. Louise Frisbie; a conditional gift of $100,000.

Stevens Institute of Technology, $50,000, from President Henry Morton.

Syracuse University, about $40,000, by the will of Justice George N. Kennedy.

Tulane University, $50,000, for library purposes, from Mrs. Caroline Stannard Tilton.

University of Chicago, $3000, by the will of Marie J. Mergier; $75,000 additional, from A. C. Bartlett.

University of Southern California, $100,000, from various donors; a conditional gift of $40,000, from Mrs. Anna Hough.

University of Virginia, an annual income of $11,000, from Mrs. Mary Austin Carroll, of Boston.

Vassar College, $28,000, by the will of Mrs. Louise Frisbie.

Washington and Jefferson (Pennsylvania) College, $100,000, from J. V. Thompson.

Wellesley College, $28,000, by the will of Mrs. Louise Frisbie.

Whitman College, a conditional gift of $50,000, from Dr. D. K. Pearson.

Yale University, $10,000, from Irwin Rew, for the Sheffield Scientific School; $25,000, from John S. Newbury, of Detroit, for an organ.

APPOINTMENTS.

Dr. Lujo Adamovič, professor of botany in the University at Belgrade. — Dr. Ludwig von Ammon of Munich, honorary professor. — M. Eugen Autran of Geneva, botanist to botanical gardens at Buenos Ayres. — S. M. Bain, professor of botany in the University of Tennessee. — Dr. Charles R. Bardeen, associate professor of anatomy in Johns Hopkins University. — Arthur W. Bean, assistant in histology and embryology in Cornell University. — Professor H. C. Beeler, state geologist of Wyoming. — Dr. Louis Beushausen, professor of geology in the mining school at Berlin. — Professor Franz Beyschlag, second director of the Prussian Geological Survey. — Dr. G. Bodländer, professor of geology in the technical school at Braunschweig. — Dr. J. Böhm, custodian of the collections of the mining school and geological survey in Berlin. — H. W. Britcher, assistant in zoölogy in the University of Maine. — W. E. Britton, state entomologist of Connecticut. — E. R. Buckley, state geologist of Missouri. — Dr. A. H. R. Buller, lecturer in botany at Birmingham University. — Charles W. Bunker, assistant in histology and embryology in Cornell University. — Louis R. Cary, assistant in biology in the University of Maine. — Professor Fridiano Cavara, professor of botany in the University at Catania. — Dr. Frederic E. Clements, adjunct professor of botany in the University of Nebraska. — Professor H. W. Conn, lecturer on agricultural biology at the Connecticut Agricultural College. — Rheinhart Parker Cowles, fellow in zoölogy in Johns Hopkins University. — Dr. Max Cremer, professor extraordinary of physiology in the University at Munich. — Dr. R. A. Daly of Harvard, assistant on the Geological Survey of Canada. — Dr. Percy M. Dawson, associate in physiology in Johns Hopkins University. — Earl Douglass, fellow in biology in Princeton University. — Mr. R. Evans of Oxford, curator of the Museum at Demarara. — Mr. M. N. Fenneman, professor of geology in the University of Colorado. — Bruce Fink, professor of geology and botany in Drake University, Iowa. — Dr. J. S. Flett, assistant in petrology on the geological survey of the United Kingdom. — Dr. Joseph Marshall Flint, professor of anatomy in the University of California. — Dr. Shepard I. France, instructor in physiology in Dartmouth College. — Adolf Fritze, professor of zoölogy in the University of Tokyo. — Dr. Karl Wilhelm Genthe, instructor in natural history in Trinity College. — Dr. Paul Goode, instructor in geography in the University of Pennsylvania. — H. H. Grau, docent for botany in the Bergen (Norway) Museum. — Dr. Emily Ray Gregory, professor of biology in Wells College, Aurora, N.Y. — Professor Eugene Haanel, of Syracuse, superintendent of mines in Canada. — Dr. E. Haunig, docent for botany in the University at Strassburg. — Dr. Charles M. Hazen, professor of biology in Richmond College, Virginia. — Dr. Tracy F. Hazen, director of the Fairbanks Museum of Natural History at St. Johnsbury, Vt. — Dr. Wilhelm Hein, docent for ethnography in the University at Vienna. — Dr. Herbert, docent

for zoölogy in the University at Heidelberg. — Bert R. Hoobler, assistant in histology and embryology in Cornell University. — F. W. Hodge, assistant in charge of office in the Smithsonian Institution. — Dr. Charles F. Hottes, instructor in botany in the University of Illinois. — J. Allen Howe, geologist on the English staff of the Geological Survey of the United Kingdom. — Dr. Alois Jenčić, assistant in vegetable physiology in the University at Vienna. — Dr. Duncan S. Johnson, associate professor of botany in Johns Hopkins University. — S. P. Jones, assistant state geologist of Georgia. — Dr. Ernst Kittl, docent for geology in the technical school at Vienna. — Dr. Alfred Koch, professor extraordinary of bacteriology in the University at Göttingen. — Dr. F. Kolbeck, professor of mineralogy in the mining school at Freiburg i. S. — Dr. A. L. Kroeber, instructor in Indian anthropology in the University of California. — Dr. August Langhofer, professor extraordinary of botany in the University at Agram, Austria. — Dr. Ralph S. Lillie, assistant in physiology in Harvard Medical School. — Dr. Walther von Lingelsheim, director of the bacteriological station in Benthen, Germany. — George H. Lyman, professor of botany in Dartmouth College. — Dr. Florence M. Lyon, associate in botany in the University of Chicago. — Dr. Albert F. Matthews, assistant professor of physiological chemistry in the University of Chicago. — Dr. Hermann Meerworth of Hamburg, assistant in the Natural History Museum in Braunschweig. — Adam Miller, fellow in biology in Princeton University. — Benjamin LeRoy Miller, fellow in geology in Johns Hopkins University. — Dr. Siegfried Mollier, professor extraordinary of anatomy in the University at Munich. — Dr. G. T. Moore of Dartmouth College, algologist to the Department of Agriculture. — H. B. Muff, geologist on the Scottish staff of the Geological Survey of the United Kingdom. — Dr. Müller, director of the newly established zoölogical garden in Halle. — Dr. Bogumil Nemec, head of the new institute of vegetable physiology in the Bohemian University at Prag. — S. P. Orth, professor of natural science at Buchtel College, Ohio. — William Osburn, instructor in zoölogy in the University of Cincinnati. — Dr. J. B. Overton, professor of biology in Illinois College. — Vládimir J. Palladin, professor of vegetable anatomy and physiology in the University at St. Petersburg. — Dr. Henry F. Reid, professor of geological physics in Johns Hopkins University. — Ralph W. Richards, fellow in biology in Tufts College. — Professor I. C. Russell, state geologist of New Jersey, to take the position next year. — Dr. Wilhelm Salomon, professor extraordinary of stratigraphy and paleontology in the University at Heidelberg. — Dr. E. Schellwein, professor extraordinary of geology and paleontology in the University at Königsberg. — Dr. Edward C. Schneider, professor of biology in Tabor College, Tabor, Iowa. — Dr. G. Senn, docent for botany in the University at Basel. — W. T. Shaw, assistant entomologist in the Iowa Agricultural Experiment Station. — Daniel Naylor Shoemaker, fellow in zoölogy in Johns Hopkins University. — Dr. F. L. Stevens, instructor in biology in the North Carolina College

of Agriculture. — H. H. Thomas, geologist on the English staff of the Geological Survey of the United Kingdom. — John J. Thornber, professor of botany in the University of Arizona. — William C. Thro, assistant in histology and embryology in Cornell University. — William George Tight, president of, and professor of geology in, the University of New Mexico at Albuquerque. — Dr. O. Uhlworm, editor of the *Botanisches Centralblatt*, librarian of the Royal Library in Berlin and chief of the German Bureau for International Bibliography. — C. E. Van Orstrand, physical geologist of the United States Geological Survey. — Dr. W. Voigt, custodian of the Natural History Museum in Bonn. — Dr. Franz Wähner of Vienna, professor of mineralogy and geology in the German technical school at Prag. — Professor Dr. Eugen Warming, director of the Danish Geological Survey. — Dr. Sho Watase, professor of zoölogy in the University of Tokyo. — Dr. Thomas L. Watson, professor of geology and botany in Denison University, Granville, Ohio. — Dr. Karl Wenle, professor of anthropology in the University at Leipzig. — Gersham F. White, assistant in histology and embryology in Cornell University. — Dr. Edwin M. Wilcox, professor of biology in the Alabama Polytechnic Institute, Auburn, Ala. — Dr. A. W. G. Wilson, assistant on the Geological Survey of Canada. — William F. Wismar, assistant in histology and embryology in Cornell University. — W. B. Wright, geologist on the Irish staff of the United Kingdom. — Dr. Rudolf Zuber, professor of geology in the University at Lemberg.

RESIGNATIONS.

Dr. E. B. Copeland, professor of botany in the University of West Virginia, legislated out of position by the regents. — Dr. C. L. Herrick, from the presidency of the University of New Mexico, on account of ill health. — F. W. Hodge, ethnologist in the Bureau of American Ethnology at Washington. — Professor Carl Wilhelm von Kupffer, from the directorship of the Anatomical Department of the University at Munich. — Dr. E. Suess, from the professorship of geology at Vienna, after nearly fifty years' service. — Dr. H. Topsöe, director of the Danish Geological Survey. — Dr. Arthur Willey, from the curatorship of the Museum at Demarara.

DEATHS.

Dr. G. A. Asp, professor of anatomy in the University at Helsingfors, April 25, aged 66. — Rev. Dr. Willis H. Barris, geologist, at Davenport, Iowa, in May, aged 79. — Alexander Becker, a Russian botanist and entomologist, April 16, aged 82. — Professor M. G. Bleicher of Nancy, known for his researches on the geology of the Vosges. — Dr. E. Bretschneider, author of several works on Chinese botany, in St. Petersburg. — Dr. Gino Ciaccio, professor of comparative anatomy in the University of Bologna. — Dr. E. W. Claypole, sometime professor of geology in Buchtel

College, Akron, Ohio, and lately professor of geology in Throop Institute, at Long Beach, Cal., August 17, aged 66. — A. Constant, student of Lepidoptera in Golfe Juan, France, May 13, aged 71. — Maxime Cornu, professor of botany in the Jardin des Plantes, at Paris, April 4, aged 58. — Adolf Fick, professor of physiology in the University at Würzburg, August 21, aged 71. — H. W. Harkness, botanist, in San Francisco, May 10, aged 80. — W. Hartwig, curcinologist, in April, in Berlin. — Rev. Moses Harvey, who added much to our knowledge of the giant squid, at St. John's, Newfoundland, September 3, aged 82. — Professor Felix Joseph Henri Lacaze-Duthiers, the eminent French zoölogist, aged 80. — Professor Gustav Lindström, paleontologist of the Royal Museum at Stockholm, May 16, aged 72. — Dr. Otto Lugger, entomologist of Minnesota since 1887, May 21. — Dr. P. Calvin Mensch, professor of biology and chemistry in Ursinus College at Collegeville, Pa., July 30. — Dr. Joshua Miller, archæologist of Arizona. — Dr. Charles Mohr, botanist, at Asheville, N.C., July 17. — P. G. von Möllendorff, a writer on the natural history of China, April 19, aged 53. — Dr. Adolf Erik Nordenskjöld, the well-known arctic explorer and naturalist, August 13, aged 68. — Miss Eleanor A. Ormerod, the British entomologist. — Dr. Antonio Piccone, algologist, in Genoa, May 21, aged 57. — Dr. Otto vom Rath, well known for his studies of myriapods and cytology, in Cologne, April 23, aged 43. — Miss Eva M. Reed, botanist and indexer in the Missouri Botanical Gardens, killed by a train July 7. — Dr. A. F. W. Schimper, professor of botany in the University at Basel, September 9, aged 45. — Dr. Domenico Stefanini, professor of bacteriology in the University at Pavia, aged 80. — Professor C. A. Tenne, custodian of the Berlin Mineralogical Museum at Bad Nanheim, aged 48. — Friedrich Tiemann, conservator of the Zoölogical Museum in Breslau. — Anthony Wilkin, an English archæologist and ethnologist, at Cairo, Egypt, May 17, aged 24. — Martin F. Woodward, demonstrator in biology in the Royal School of Science at South Kensington, drowned September 15.

CORRESPONDENCE.

Editor of the American Naturalist:

SIR: — A slight correction should be made in my "Notes on Living Nautilus," which appeared in the October number of the *American Naturalist.* I notice that on p. 828 the block of cuts 6, 7, and 8 has been set so that the animals seem to be looking somewhat upward. To appear accurately, the three figures should be rotated downward, clock-hand fashion, each about thirty degrees.

BASHFORD DEAN.

DEPARTMENT OF ZOÖLOGY,
COLUMBIA UNIVERSITY, NEW YORK,
November 12, 1901.

(*No. 419 was mailed November 18.*)